2010

IMPACT OF DIETARY DIVERSIFICATION ON INVASIVE SLUGS AND BIOLOGICAL CONTROL WITH NOTES ON SLUG SPECIES OF KENTUCKY

Anna K. Thomas
University of Kentucky, annat@wcs.eddu

ABSTRACT OF THESIS

IMPACT OF DIETARY DIVERSIFICATION ON INVASIVE SLUGS AND BIOLOGICAL CONTROL WITH NOTES ON SLUG SPECIES OF KENTUCKY

Increasing introductions of non-native terrestrial slugs (Mollusca: Gastropoda) are a concern to North American regulatory agencies as these generalists impact the yield and reduce the aesthetic value of crop plants. Understanding how the increase in diversification in North American cropping systems affects non-native gastropods and finding effective biological control options are imperative for pest management; however, little research has been done in this area. This study tested the hypothesis that dietary diversification affects the biological control capacity of a generalist predator and allows the slug pest *Deroceras reticulatum* (Müller) (Stylommatophora: Agriolimacidae) to more effectively fulfill its nutritional requirements. Results showed no significant correlations between dietary diversification and slug development; however, this was likely due to the addition of romaine lettuce to all treatments. The study also showed that dietary diversification had no significant effect on *D. reticulatum* egg production, with self-fertilizing slugs consistently having significantly higher egg production than outcrossing slugs. Most significantly, this research demonstrated reductions in plant damage by *D. reticulatum* in treatments containing the North American carabid beetle *Scarites quadriceps* Chaudoir (Coleoptera: Carabidae) with the presence of alternative prey having no effect, supporting its use in biological control efforts in spite of its generalist feeding habits.

KEYWORDS: dietary diversification, fecundity, biological control, terrestrial slug, Carabidae

Anna K. Thomas

May 7, 2010

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By

Anna K. Thomas

James D. Harwood
Director of Thesis

Chuck W. Fox
Director of Graduate Studies

May 7, 2010
Date

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THESIS

Anna K. Thomas

The Graduate School

University of Kentucky

2010

IMPACT OF DIETARY DIVERSIFICATION ON INVASIVE SLUGS AND BIOLOGICAL CONTROL WITH NOTES ON SLUG SPECIES OF KENTUCKY

THESIS

A thesis submitted in partial fulfillment of the
requirements for the degree of Master of Science in the
College of Agriculture
at the University of Kentucky

By

Anna K. Thomas

Lexington, Kentucky

Director: Dr. James D. Harwood, Assistant Professor of Insect Ecology

Lexington, Kentucky

2010

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Dedication

This thesis is dedicated to my mother. Though she can no longer be with me physically, her love and support carry me through my life and career.

ACKNOWLEDGMENTS

I am grateful to my graduate advisor, Dr. James D. Harwood, for all of his patience, guidance, and support. His door has always been open and his advice has been invaluable throughout my graduate career. Dr. Harwood has also furthered my education and experience by allowing me the opportunity to travel to conferences and meetings where I have been able to showcase my research and the knowledge I have gained since joining the university. I would like to thank my committee members Drs. Daniel A. Potter and John J. Obrycki for their advice and assistance on this project. They have demonstrated all of the qualities attributable to excellent educators: patience, wisdom, and enthusiasm. Dr. Potter also allowed me access to tools and equipment in his laboratory without which completion of my work would have been impossible. I would like to acknowledge the following members of my lab who have been not only colleagues, but friends: Mike Eskelson, Julie Peterson, Kelton Welch, Eric Chapman, Susan Romero, Mark Adams, and Jessica Houle. Without their encouragement and help, I would not have been able to complete my research. I would like to thank the Kentucky Society of Natural History for funding for my faunistic survey and the University of Kentucky Department of Entomology for a research assistantship. I would also like to thank the Kentucky Department of Parks for assistance and permits for collections in State Parks and Reserves, everyone who collected slugs for this research and allowed collecting on their property, and the team at the University of Kentucky Horticultural Research Farm for allowing me to use space for my miniplot study. Finally, I would like to thank my family and friends who have always encouraged me to work towards my goals and enjoy myself in the process. Without your strength, I would not have reached this point.

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Chapter One: Introduction

1.1. Terrestrial Slug Morphology

Terrestrial slugs are a polyphyletic group derived from snails. The loss of an exterior shell for most slug species means the animal's body is capable of compression which allows it to enter small crevices. This allows them to retreat deep into the soil to avoid unfavorable environmental conditions or hide from surface-active predators. The body wall of the slug is indicative of the animal's lifestyle, as slugs with a thicker body wall generally spend more time below ground (South 1992). Each slug has a mantle behind its head that covers approximately one-third of its dorsal surface and an internal shell just beneath the mantle. The slug breathes through a pneumostome that opens into a cavity in its mantle and the position of the pneumostome can help identify different families of slugs. Another identifying trait of the slug is a keel on the tail of some slug species. Depending on the slug family, the keel may stop before the mantle or it may continue to the mantle. Certain slug families lack this distinguishing characteristic and instead have a posterior mucus gland (South 1992).

Since a slug's skin is sensitive to water loss and chemicals, slugs use mucus to lubricate and protect themselves from the elements (South 1992) and to serve several other functions, such as aiding in locomotion and playing a role in courtship and mating. Mucus is also used in defense as most slug species may secrete copious amounts of the substance in order to make themselves unpalatable or make it difficult for predators to hold them (Gordon 1994). A slug's mucus may also be helpful in identifying species.

For example, members of the *Arion hortensis* (Férussac) (Stylommatophora: Arionidae) aggregate produce yellow mucus (Runham and Hunter 1970).

A slug usually has two pairs of tentacles, one of which being responsible for vision. A study of the eye of *Deroceras reticulatum* (Müller) (Stylommatophora: Agriolimacidae) showed a low number of photoreceptor cells, indicating that this species' eye creates poor retinal images and is more useful in detecting changes in light intensity, suitable to a nocturnal animal (Newell and Newell 1968). An accessory retina in the eye of a slug is believed to be an infrared receptor, which can sense heat even when the optical tentacles are withdrawn into the body (Newell and Newell 1968, Kerkut and Walker 1975). In a study of the eyes of these organisms, Eakin and Brandennburger (1975) described two types of photoreceptor cells and suggested differences in the Type I photoreceptor cells between light-tolerant and light-avoiding species.

1.2. Geographic Distribution

Terrestrial slugs have a worldwide distribution and are present in several different habitats including gardens, parks, forests, and agricultural areas. Generally, invasive species are associated with people and native species are found in more remote, undisturbed locations such as old growth forests (Kappes 2006). Slugs native to North America are those in the subfamily Ariolimacinae and the genera *Prophysaon* (Stylommatophora: Arionidae), *Anadenulus* (Stylommatophora: Arionidae), *Philomycus* (Stylommatophora: Philomycidae), and *Pallifera* (Stylommatophora: Philomycidae) (South 1992). The most common non-native slugs in North America include *Arion ater* (Linnaeus), *Arion circumscriptus s.s.* (Johnston), *A. hortensis*, *Arion intermedius*

(Normand), *Deroceras agreste* (Linnaeus), *Deroceras laeve* (Müller), *D. reticulatum*, *Limax maximus* (Linnaeus) (Stylommatophora: Limacidae), and *Milax gagates* (Draparnaud) (Stylommatophora: Milacidae) (Gordon 1994). Other non-native slug species in North America are the *Arion subfuscus* (Draparnaud)/*fuscus* (Müller) complex (Gordon 1994), *Deroceras panormitanum* (Lessona and Pollonera) and *Tandonia budapestensis* (Hazay) (Stylommatophora: Milacidae) (Reise *et al.* 2006). *D. laeve* is considered both native and non-native to North America as certain populations are pre-Columbian, while others were introduced more recently (South 1992). See Table 1.1 for slug species recorded in Kentucky.

Table 1.1 Non-native terrestrial slug species recorded in Kentucky. [1]

Slug Species
Arion hortensis (Férussac) (Stylommatophora: Arionidae)
Arion intermedius (Normand) (Stylommatophora: Arionidae)
Arion subfuscus s.s. (Draparnaud) (Stylommatophora: Arionidae)
Deroceras laeve (Müller) (Stylommatophora: Agriolimacidae)
Deroceras reticulatum (Müller) (Stylommatophora: Agriolimacidae)
Lehmannia valentiana (Ferussac) (Stylommatophora: Limacidae)
Limax flavus (Linnaeus) (Stylommatophora: Limacidae)
Limax maximus (Linnaeus) (Stylommatophora: Limacidae)
Milax gagates (Draparnaud) (Stylommatophora: Milacidae)

[1] Data were obtained and summarized from Branson and Batch 1969, Mc Donnell *et al.* 2009, Thomas and Harwood unpublished data.

Due to global trade and international trade agreements, invasions by non-native gastropod species are becoming more common. Robinson (1999) listed 4,900 gastropods intercepted on their way into the United States from 100 countries between 1993 and 1998 and there are over eighty established non-native slug and snail species in the United States and Canada (Mc Donnell *et al*. 2009). This problem poses very serious threats to North American horticulture and agriculture (Robinson and Slapcinsky 2005, Mc Donnell *et al*. 2009). Therefore, Robinson (1999) suggested that surveys of urban and suburban areas are essential to identify invasive gastropods soon after colonization and thus allow rapid implementation of management practices. Reise *et al*. (2006) stated that without knowing the distribution of a non-native species or if it is present in the United States, the USDA Animal and Plant Health Inspection Service's Plant Protection and Quarantine division (APHIS PPQ) cannot determine whether a gastropod species that is intercepted on an imported product represents a new agricultural or environmental threat. The ease with which gastropods can be unintentionally transported with plants is often seen. For example, one cardboard box of ash saplings shipped from California to Massachusetts in September 2005 was found to contain eight species of gastropod (five snail species and three slug species) and several eggs (Gary Bernon, USDA-APHIS, pers. comm.)

1.3. Predators and Parasites

Slugs have many predators all over the world, including many potential biological control agents. These predators include surface-active and subterranean vertebrate and invertebrate species. For a list of documentedsurface-active vertebrate predators, see Table 1.2.

Table 1.2. Surface active vertebrate predators of terrestrial slugs. [2]

Slug Predators
Common shrew (*Sorex araneus* Linnaeus) (Soricomorpha: Soricidae)
Badger (Carnivora: Mustelidae)
Hedgehog (Erinaceomorpha: Erinaceidae)
Frogs and toads (Anura)
Salamanders (Caudata)
Slow-worm lizards (*Anguis fragilis* Linnaeus) (Squamata: Anguidae)
Redbelly snake *Storeria occipitomaculata* (Storer) (Squamata: Colubridae)
Brown snake *Storeria dekayi* (Holbrook) (Squamata: Colubridae)
Garter snakes (Squamata: Colubridae)
Blackbird *Turdus merula* Linnaeus (Passeriformes: Turdidae)
Fieldfare *Turdus pilaris* Linnaeus (Passeriformes: Turdidae)
Thrush *Turdus ericetorum* (Turton) (Passeriformes: Turdidae)
Redwing *Turdus iliacus* Linnaeus (Passeriformes: Turdidae)
Starling *Sturnus vulgaris* (Linnaeus) (Passeriformes: Sturnidae)
Rock dove *Columba livia* (Gmelin) (Columbiformes: Columbidae)
Wryneck *Jynx torquilla* (Linnaeus) (Piciformes: Picidae)
Red grouse *Lagopus scoticus* (Galliformes: Tetraonidae)

[2] Data were obtained and summarized from Elliott 1967 and South 1992.

Surface active invertebrate predators of slugs include Lampyridae (Coleoptera), Carabidae (Coleoptera), Drilidae (Coleoptera), Calliphoridae (Diptera), Sciomyzidae (Diptera), Phoridae (Diptera), mites (Acari), other gastropods, flatworms (Platyhelminthes) [reviewed in detail by South 1992], and centipedes (Chilopoda) (Lawrence 1939, Tod 1973). Cockroaches (Blattaria) have been recorded to feed on eggs of slugs in the genus *Veronicella* (Veronicellidae) (Grasse 1968). Other invertebrates shown to feed on slugs are spiders (Araneae) and their close relatives, the Opiliones (Nyffeler and Symondson 2001) although very little information is available with regard to the frequency or importance of such trophic interactions in the field.

Ground beetles (Coleoptera: Carabidae) are well-known invertebrate predators of slugs (Davies 1953, Mead 1961, Stephenson and Knutson 1966, Tod 1970, Cornic 1973, Tod 1973, Baronio 1974, Mead 1979, Symondson *et al.* 1996, 2000, McKemey *et al.* 2001, Paill *et al.* 2002, Symondson *et al.* 2002a, 2002b, Oberholzer *et al.* 2003, Chabert and Beaufreton 2004, Chabert and Gandrey 2004, Choi *et al.* 2004, Dodd *et al.* 2004, Foltan *et al.* 2004, King *et al.* 2004). One species of *Carabus* (Coleoptera: Carabidae) is known to tear open the skin and feed on the viscera of *Lehmannia marginata* (Müller) (Taylor 1902-1907). *Carabus violaceus* (Fabricius) has been observed killing *A. hortensis* (Moore 1934), *D. reticulatum*, and *M. gagates* (Tomlin 1935). *Calosoma frigidum* (Kirby) (Coleoptera: Carabidae) eats *A. ater* and other slugs (Poulin and O'Neill 1969) and *Pterostichus melanarius* (Illiger) (Coleoptera: Carabidae), *Abax parallelepipedus* (Piller and Mitterpacher) (Coleoptera: Carabidae) (Johnson 1965), and *Feronia madida* (Fabricius) (Coleoptera: Carabidae) (Warley 1970) also prey on slugs. In Kentucky, the native carabid beetle species *Scarites quadriceps* Chaudoir (Coleoptera:

Carabidae), has been observed feeding on non-native slug species and may be an effective conservation biological control agent in the state. In the laboratory, slugs have been shown to avoid the chemical trail left behind by carabid beetles, which is further evidence supporting the likely impact carabids have on slug numbers (Armsworth *et al.* 2005) and their potential as biological control agents of these pest species.

In addition to invertebrate predators, slug populations are also affected by parasites such as the parasitic nematode *Phasmarhabditis hermaphrodita* (Schneider) (Nematoda: Rhabditidae), which is currently used as a mass-produced biological control agent against pestiferous slug species in Europe (Iglesias *et al.* 2003, MacMillan *et al.* 2006, Rae *et al.* 2006, Hapca *et al.* 2007). *P. hermaphrodita* larvae search the soil for a slug host from the families Arionidae, Milacidae, Limacidae, and Vaginulidae (Stylommatophora). Once they find a host, they enter the slug's dorsal integumental pouch just behind the mantle and inject a symbiotic bacterium. This bacterium kills the slug and the nematodes develop and reproduce (Rae *et al.* 2006, Hapca *et al.* 2007). Rae *et al.* (2006) showed that the nematodes follow cues in the slug's foot and mantle mucus as well as in the slug's feces. Nematodes are more attracted to dead than live hosts and they are indifferent as to whether the host was previously infected. Hapca *et al.* (2007) demonstrated that *P. hermaphrodita* larvae will alter their behavior when they encounter cues left behind by a slug. When the nematode is placed away from the attractant, the larvae increase their speed in the direction of the cue and when the nematode is placed on the attractant, its speed decreases. Finally, the turning angle distributions studied offer more proof that the nematode will follow a slug's mucus trail.

1.4. Feeding

Slugs eat a variety of foods including plants, fungi, lichen, annelids, insects, feces, carrion, and other slugs (Gordon 1994). Most garden slugs feed near the ground or just below its surface, the main exception being *D. reticulatum*, which will crawl up plants to feed (Barnes and Weil 1945). Some garden plants attacked by slugs include cabbages (*Brassica oleracea* var. *capitata* Linnaeus) (Brassicales: Brassicaceae), leeks [*Allium ampeloprasum* var. *porrum* (Linnaeus)] (Asparagales: Alliaceae), potatoes (*Solanum tuberosum* Linnaeus) (Solanales: Solanaceae), onions (*Allium cepa* Linnaeus), primulas (Ericales: Primulaceae), campanulas (Asterales: Campanulaceae), saxifrage (Saxifragales: Saxifragaceae), scarlet runner bean (*Phaseolus coccineus* Linnaeus) (Fabales: Fabaceae), Michaelmas daisy [*Symphyotrichum novae-angliae* (Linnaeus)] (Asterales:Asteraceae), artichoke (*Cynara cardunculus* Linnaeus) (Asterales: Asteraceae), and strawberries (Rosales: Rosaceae) (Barnes and Weil 1945). Slugs will also eat several agricultural plants such as wheat (Poales: Poaceae), sunflower (*Helianthus annuus* Linnaeus) (Asterales: Asteraceae), corn (*Zea mays* Linnaeus) (Poales: Poaceae), and soybean [*Glycine max* (Linnaeus)] (Fabales: Fabaceae) (Faberi 2006). For example, *D. reticulatum* has the capacity to damage up to a third of winter wheat (*Triticum hybernum* Linnaeus) (Poales: Poaceae) seeds and seedlings in the United Kingdom and other temperate climates (Port and Port 1986, Glen 1989, Brooks *et al*. 2005) and *A. subfuscus* has been reported as being responsible for stand loss in soybean crops in the United States (Hammond *et al.* 1999). Slugs damaging potatoes, sugar beets (*Beta vulgaris* Linnaeus) (Caryophyllales: Amaranthaceae), barley (*Hordeum vulgare* Linnaeus) (Poales: Poaceae), and oilseed rape (*Brassica napus* Linnaeus) have also been recorded [reviewed in detail by South 1992]. For this reason, they are considered major agricultural pests (Sproston *et al*. 2005). To exacerbate their pest status, slugs also vector several plant diseases. Sproston *et al.* (2005) showed that *D. reticulatum* could act as vectors of *Escherichia coli* 0157 (Migula) Castellani and Chalmers (Enterobacteriales: Enterobacteriaceae) by carrying the pathogen from sheep feces to vegetables. Their research showed that once a slug becomes contaminated with *E. coli* through contact and/or ingestion, it persists on the slug and in the slug's system for several days. This is more than enough time for the animal to transfer the *E. coli* to vegetables through direct contact or in its feces.

Sometimes, slug feeding is beneficial as they tend to feed on wilting or dying plants (as well as the bark of fallen trees) and thus they play an extremely important role in detrital food webs and provide ecological services in natural compost heaps. The fact that many species have the capacity to feed on carrion can be beneficial, because they render noxious particles harmless (Tenney 1877). The sacoglossan sea slugs (Mollusca: Opisthobranchia) *Placida dendritica* (Alder and Hancock), *Placida aoteana* (Powell), and *Elysia viridis* (Montagu) are extremely beneficial, because they feed on the invasive shoreline plant *Codium fragile* ssp. *tomentosoides* (van Goor) (Chlorophyta), frequently feeding on the invasive over native plants in Scotland, Ireland, Australia, and Tasmania (Trowbridge 2004).

1.5. Slugs as Horticultural and Floricultural Pests

Slugs are well known agricultural pests in Great Britain, capable of damaging whole fields of cabbage, wheat, and other plants (Anonymous 1905). Perhaps less well known is the fact that these animals are important pests in the horticultural and floricultural industries. Slugs will frequently damage brassicas, carrots (*Daucus carota* Linnaeus) (Apiales: Apiaceae), celery (*Apium graveolens* Linnaeus) (Araliales: Apiaceae), and runner, broad (*Vicia faba* Linnaeus), and French (*Phaseolus vulgaris* Linnaeus) beans (Fabales: Fabaceae). They will also damage strawberries, cucumbers (*Cucumis sativus* Linnaeus) (Cucurbitales: Cucurbitaceae) and chicory (*Cichorium intybus* Linnaeus) (Asterales: Asteraceae). Most damage occurs at the seedling stage (Anonymous 1979). On flowering plants and ornamentals, slugs will most often attack bulbs, corms, and tubers and young shoots emerging from herbaceous perennials. They will also eat mature foliage and flowers (Eaton and Tomsett 1976, Anonymous 1979).

Slug pest status is augmented by the fact that they have been shown to transport several plant diseases. Wester *et al.* (1964) reported that slugs are capable of transporting downy mildew (Peronosporales:Peronosporaceae) to lima beans (*Phaseolus lunatus* Linnaeus) (Fabales: Fabaceae) and Hering (1969) reported that *D. reticulatum* and *A. hortensis* spread the fungus *Botrytis* (Helotiales: Sclerotiniaceae) along grapevines (Vitales: Vitaceae). Slugs are also vectors of the brassica dark leaf spot [*Alternaria brassicicola* (Schwein.) Wiltshire] (Pleosporales: Pleosporaceae) (Hasan and Vago 1966), carrot licorice rot [*Mycocentrospora acerina* (Hartig) Deighton] (Ascomycetes) (Dawkins *et al*. 1985), and bacterial soft rot [*Pectobacterium carotovorum* (Jones) Waldee] (Enterobacteriales: Enterobacteriaceae) (Dawkins *et al.*

1986). Thus, the impact of non-native slugs on horticultural and floricultural crops is more than simple plant feeding; many complex and coupled factors are interacting and contributing to potential pest damage within these systems. Therefore, it is important to find economical and efficient ways to control these non-native pests. Due to their nocturnal habits and the ease with which slug herbivory can be mistaken for damage from other North American pest species, there is a dearth of slug research in the Nearctic region, compared to the Western Palearctic region. It is therefore critical to further understand the impact of slugs in other regions in order to find efficient means of controlling these pests.

1.6. Slugs and Natural Enemies in Urban Environments

Barnes and Weil (1944, 1945) performed a survey of fifty gardens in Hertfordshire, United Kingdom twenty-five miles north of London, United Kingdom from 1940 to 1943. They found that some of the most common species of slugs include *A. ater*, *A. hortensis*, *A. subfuscus*, *Milax gracilis* (Leygig), *Milax sowerbyi* (Ferussac), and *D. reticulatum* (*A. hortensis* refers to the *A. hortensis* complex and *A. subfuscus* refers to the *A. subfuscus* complex). In fact, two non-native slugs present in North America, *D. reticulatum* and *A. hortensis*, were found in every garden on almost every sampling date. Lyth (1972) looked at the species of slugs present in a garden in Kent, United Kingdom and found *D. reticulatum*, *T. budapestensis*, *A. hortensis*, *A. fasciatus*, *A. subfuscus*, *A. ater* and *M. sowerbyi* and Atkinson (1979) recorded *T. budapestensis*, *D. reticulatum*, and *A. hortensis* as common garden pests in allotment gardens around Leeds, United Kingdom. A study in the Netherlands also found seven slug species present in gardens and arable land, including *D. reticulatum*, *A. hortensis*, *A. ater*, *A. circumscriptus*, and *L. maximus* (Bruijns *et al.* 1959). The extent with which these species can colonize urban and residential environments augments their pest status, making the need for efficient control measures more immediate.

As stated above, carabid beetles are common predators of slugs. There are over 40,000 species of ground beetles worldwide (Wiedenmann *et al.* 2004), many occurring in North America. It is highly probable that these predators can be used in horticultural and floricultural plots as a form of conservation biological control. Sadof *et al*. (2004) showed that implementation by Master Gardeners of biological control can significantly reduce the amount of pesticides used in gardens. Due to the dangers associated with pesticide use and storage, an alternative such as biological control could be extremely beneficial to homeowners. Habitat manipulation is a tool horticulturalists and floriculturalists can use to control slug numbers by encouraging native predators. In research conducted in Illinois and Indiana, Wiedenmann *et al*. (2004) looked at ground beetle assemblages in mulched and non-mulched garden plots. For this research, potato plots of Master Gardener volunteers were either mulched with straw or left unmulched. Wiedenmann *et al.* found that *species diversity* was greater in unmulched plots, but the *number of beetles* was higher in mulched plots. This study showed that manipulation of habitats (even small habitats such as home gardens) to enhance predator numbers and species distributions may help to control pest numbers. However, alteration of a habitat should be done carefully, as any change may also benefit the pests (Wiedenmann *et al*. 2004).

1.7. Management

Farmers and gardeners use different methods to control slug damage including beer traps, copper barriers, and salt (Gordon 1994), as well as alternative food sources (Cook *et al.* 1996) such as red clover (*Trifolium pratense* Linnaeus) (Fabales: Fabaceae) (Brooks *et al.* 2005) and molluskicide treatments (Iglesias *et al.* 2003, Bieri *et al.* 2004, Glen *et al.* 2004, Schuder *et al*. 2004). Cook *et al.* (1996) tested the palatabilities of different wheat cultivars and agricultural weeds to *D. reticulatum* to see if alternative food sources would reduce damage to winter wheat crops. The study showed that slugs have no preference to specific wheat cultivars, but they do show a preference to different weed choices, sometimes choosing weeds over wheat. These results indicate that planting certain weed species among wheat could affect levels of wheat herbivory and may be a good form of integrated pest management.

Brooks *et al.* (2005) investigated whether use of red clover as an alternative food source is as successful at reducing slug herbivory on winter wheat as metaldehyde pellets and found that metaldehyde is more effective at reducing herbivory on wheat seeds than red clover. However, they also found that red clover and metaldehyde each reduce slug herbivory on wheat *seedlings* by 55% compared to no treatment at all. This supports the findings of Cook *et al.* concerning the benefits of using an alternative food source to reduce slug herbivory. Slugs are generalist herbivores and will practice compensatory feeding by broadening their diets in order to gain the nutrients needed for development and reproduction. Therefore, offering slugs an alternative food choice could decrease slug herbivory by lowering the amount of feeding damage on certain agricultural crops. Conversely, if the alternative food choice is nutrient-rich, diversification of slug diet may increase the fecundity and therefore the population size of pest species, increasing long term feeding damage of these organisms in the crop system.

1.8. Objectives

The objective in Chapter 2 of this study was to demonstrate the quantitative effects of dietary diversification on the survival and growth of *D. reticulatum*. It tested the hypothesis that a diverse diet is beneficial for this species and allows these herbivores to fulfill their nutritional requirements more effectively than a single-source diet through dietary mixing. The objective of Chapter 3 was to demonstrate the quantitative effects of treatment food and dietary diversification on the fecundity of *D. reticulatum* in individual (self-fertilizing) and paired (outcrossing) experimental conditions. It tested the hypothesis that egg production and viability would increase and time to hatching would decrease when slugs had the opportunity to outcross. It also tested the hypothesis that fecundity would increase in treatments with greater dietary diversification since it would allow these generalist feeders to fulfill their nutritional requirements more effectively than single-source diets. The objective of Chapter 4 was to quantify the biological control capacity of a key native North American generalist predator, *S. quadriceps*, against non-native slug populations and the subsequent effect on plant growth and development. This experiment compared herbivory on young *Hosta* plants by the non-native slug *D. reticulatum* and the effect of *S. quadriceps* on levels of plant damage and tested the hypothesis that the presence of carabid beetles significantly reduces slug herbivory on plants. Furthermore, the hypothesis that dietary diversification in predators will disrupt the slug – carabid trophic pathway, thus leading to an increase in plant damage, was examined by including *Musca domestica* (Linnaeus) (Diptera: Muscidae) pupae as an alternative food source for the beetles.

Chapter Two: Effects of dietary diversification on survivorship, development, and egg production in the non-native mollusk, *Deroceras reticulatum* (Müller)

2.1. Summary

Many studies have indicated that survival, development, and fecundity of polyphagous organisms are affected by diet and dietary diversification. One group of generalist feeders, terrestrial slugs, eat a wide variety of foods including, but not limited to, healthy and decaying plant material, fungi, algae, lichens, moss, flesh, feces, bread products, and corn products. Through their polyphagous feeding habits, terrestrial slugs have been shown to broaden their diets in order to gain the nutrients they need for development and reproduction. Due to the diverse feeding habits of these organisms, along with their ability to transmit several plant diseases, they are considered agricultural, horticultural, and floricultural pests throughout much of the world. As introductions of non-native gastropods into North America become more common, land managers and plant growers, both commercial and residential, face a greater threat posed by these pestiferous species. The situation is exacerbated by the diversification of America's agricultural and horticultural industries and the movement towards organic farming practices, which may benefit generalist herbivore pests. This study evaluated the effect of dietary diversification on the development of *D. reticulatum*, a common slug pest. It tested the hypothesis that a diverse diet is beneficial for this species and allows these animals to fulfill their nutritional requirements more effectively than a single-source diet. The hypothesis was tested by feeding juvenile slugs a diet ranging in diversity levels from one to four *Hosta* varieties. Leaf characteristics of all plant types were measured to provide a possible explanation for any differences in slug development and biomass was

used to measure the development of the animals. Due to high slug mortality, organic romaine lettuce was added to each *Hosta* treatment and an additional control of organic cabbage was included. This research found that there were no significant correlations between dietary diversification and *D. reticulatum* development. However, the lack of significance between treatments was likely due to the addition of romaine lettuce to all *Hosta* treatments. The only treatment in this study showing significantly different mean total and daily differences in slug biomass was the cabbage control. It is likely a combination of significantly higher plant thickness and toughness in combination with the chemical composition of cabbage that significantly reduced slug development on this species. The results of this study imply that, at least in residential gardens or floricultural fields, diversification of *Hosta* varieties does not have a significant effect on the life history of *D. reticulatum*. However, due to the standardization of diets in the study, more research is needed to make final determinations.

2.2. Introduction

There are many studies showing that the survival, development, and fecundity of polyphagous herbivores are affected by diet and dietary diversification (Sonoda *et al*. 1991, Moreau *et al.* 2006, Amaresekare *et al.* 2008, Unsicker *et al*. 2008, Wang *et al*. 2008) and herbivores have to balance their intake of different nutrients in order to develop successfully (Behmer and Joern 1993, Lee *et al*. 2002, Berner *et al*. 2005). According to the nutrient complementation hypothesis, single plant species do not contain all the nutrients necessary for herbivore growth and therefore herbivores are more likely to obtain all of the nutrients they need by broadening their diet (Pulliam 1975, Rapport 1980). This form of compensatory feeding has been shown in a number of studies involving insect herbivores (Berner *et al.* 2005, Lee *et al.* 2004, Takeuchi *et al.* 2005). A second form of compensatory feeding is the ontogenetic niche concept, which states that resource use may also depend on an organism's developmental stage (Unsicker *et al.* 2008). For example, as an herbivore grows, it may change its host plant to account for new nutritional requirements. A third theory of compensatory feeding states that herbivores may utilize different host plants in order to avoid the detrimental effects of plant secondary chemicals. The toxin dilution hypothesis states that host switching allows herbivores to consume a lower dosage of toxins or deleterious compounds produced by particular plant species and therefore experience less of their negative effects (Freeland and Janzen 1974, Behmer *et al*. 2002, Singer *et al*. 2002, Marsh *et al*. 2006). These complementary theories show that a diverse diet is beneficial and favored in many biological systems.

Terrestrial slugs eat a wide variety of foods including, but not limited to, healthy and decaying plant material, fungi, algae, lichens, moss, flesh, feces, bones, bread products, corn products, old tea leaves, and coffee grounds (Barnes and Weil 1945). As demonstrated through an evaluation of carbon and nitrogen isotopes in which slugs of the families Milacidae, Agriolimacidae, and Arionidae all contained similar levels of $\delta^{13}C$ and $\delta^{15}N$, the feeding habits of these three speciose families are very similar. There is also evidence to suggest that *D. reticulatum* shifts from fresh to decaying plant material as it matures (Schmidt *et al*. 2004). Some terrestrial slugs have been shown to practice compensatory feeding as defined by the nutrient complementation hypothesis. Cook *et al.* (2000) demonstrated that *D. reticulatum* will choose a new food item over a familiar one in order to fulfill nutritional requirements not satisfied by their earlier diet. Many common slug species, such as *D. reticulatum*, are agricultural and garden pests due to their diverse dietary habits. In fact, slugs are the main pests of *Hosta* plants, the most commonly planted perennial in the United States.

Hosta (Asparagales: Agavaceae) is a genus containing sixty-seven species of herbaceous perennial plants native to northeast Asia. They are generally shade-tolerant plants with broad leaves that grow from corms or rhizomes. The popularity of this plant has led to over 3,000 cultivar varieties (Hosta Species Update, www.hostalibrary.org/species/index.html). *Hosta* cultivars are commonly divided up based on color. The main color groups include green, gold, blue, and variegated and their sizes range from miniature to large (New Hampshire Hostas, www.nhhostas.com). According to growers, the *Hosta* varieties thought to be most susceptible to slug damage seem to be those with thin leaves and those with leaves that grow close to the ground. Several *Hosta* varieties are described as slug resistant, especially blue *Hosta* plants, which are coated with a waxy substance that give the leaves their blue tint (Ohio State University Extension Fact Sheet, Growing Hostas, ohioline.osu.edu/hyg-fact/1000/1239.html). However, no quantitative studies have ever shown the nutritional composition or the physical structure of the leaves of *Hosta* varieties which may explain why some seem to have resistance to slug damage, while others do not.

There has also been very little research examining the role a diverse diet may play in the life history of land mollusks. The objective of this study was to demonstrate the quantitative effects of dietary diversification on the growth, fecundity, and survival of *D. reticulatum*, a common pest to ornamental plants, particularly *Hosta* plants. To test the hypothesis that a diverse diet is beneficial for this species by allowing them to fulfill their nutritional requirements more effectively than a single-source diet through dietary mixing, juvenile slugs were fed a diet ranging in diversity levels from one to four *Hosta* varieties. Leaf characteristics (carbon, nitrogen, and water content, as well as thickness and toughness) of all plant types were measured to provide a possible explanation for any differences in slug development and fecundity. Changes in biomass were used to measure the development of the animals. *D. reticulatum* is an hermaphroditic species with the ability to self-fertilize, therefore, when the slugs reached sexual maturity, they had the potential to produce eggs. The number of eggs produced, their hatching success, and time to hatching were used to measure fitness. The experiment continued through the developmental and reproductive period of the slugs.

2.3. Materials and Methods

2.3.1. Slug Collection and Maintenance

Adult *D. reticulatum* were collected from habitats in Lee County, Kentucky (37°31'N 83°43'W), the Horticultural Research Farm of the University of Kentucky (37°58'N 84°32'W) and the University of Kentucky Spindletop Research Farm (38°07'N 84°30'W), both located in Lexington, Fayette County, Kentucky. Slugs were maintained as breeding pairs in plastic containers (100 mm diameter, 40 mm wide) at 20°C on a 16:8 light:dark cycle. They were fed an *ad libitum* supply of fresh organic cabbage, romaine lettuce (*Lactuca sativa* Linnaeus var. *longifolia*) (Asterales: Asteraceae), carrot, and potato. The floors of the containers were lined with wet cotton (U.S. Cotton Co., Lachine, Québec, Canada) and six small air holes created by inserting sharp forceps into side of the plastic container provided sufficient ventilation for the health of the animals.

Eggs were collected weekly and egg batches were kept separately in plastic containers as detailed above. The floors of the containers were lined with wet cotton, as above, and a hole (2 cm^2) covered with fine mesh provided sufficient ventilation to prevent condensation. Hatchling slugs were randomly assigned to one of twelve treatments and kept individually as detailed above and fed an *ad libitum* supply of fresh treatment food (see below).

2.3.2. Measurement of Plant Characteristics

Plant traits were measured to quantify differences in leaf characteristics of fresh organic cabbage, romaine lettuce, *Hosta* 'Fragrant Blue' (P. Aden 1988), *Hosta* 'Guacamole' (R. Solberg 1994), *Hosta* 'Red October'(R. Herold NR), *Hosta* 'So Sweet'(P. Aden 1986), and *Hosta* 'Sun Power'(P. Aden 1986). The five varieties of *Hosta* were obtained from New Hampshire Hostas (South Hampton, NH, USA) and Bloomin' Designs Nursery (Auburn, GA, USA) when the plants were approximately 18 months of age. Once the plants outgrew their shipment containers they were transplanted into 25.4 cm pots in Lambert LM-3 general purpose potting mix (Lambert Peat Moss Inc., Québec, Canada). The plants were maintained in a greenhouse at approximately 25°C (day) and 21°C (night) under 60% shade (DeWitt knitted black shade cloth, DeWitt Co., Sikeston, MO, USA) on a 14:10 L:D cycle . The plants were watered liberally every two days. No fertilizer was used. Cabbage and romaine lettuce were obtained from a local grocer as needed for the trials.

Plant measurements were taken using a single newly expanded leaf from ten replicates of each cultivar. In the case of the cabbage and romaine lettuce, one head served as one replication so one leaf from each of ten heads per plant type were used. Both toughness and thickness measurements were taken on the same leaf for each of the ten replicates, with thickness measurements taken first. Leaf thickness was measured with a Model IDC Series 543 Digimatic Indicator (Mitutoyo Corporation, Kawasaki, Kanagawa, Japan) and leaf toughness was measured with an EG2 Digital Force Gauge Penetrometer (Mark-10, Copiague, NY, USA). One point on either side of the mid-vein was measured in the middle of each leaf to get an average value for the overall thickness and toughness. Leaf veins were not measured.

Carbon and nitrogen content were measured with a flash elemental analyzer series 1112 (Thermo Fisher Scientific Inc., Waltham, MA, USA) after leaves had been dried for 48 hours at 50°C in a Model 280 isotemp vacuum oven (Fisher Scientific, Pittsburgh, PA, USA) and ground using a pulverisette 23 mini-mill (Fritsch GmbH, Idar-Oberstein, Rhineland-Palatinate, Germany). Each leaf was ground for 1 minute at 40 oscillations per second.

Water content was analyzed by comparing leaf biomass before and after desiccation in the vacuum oven for 48 hours at 50°C. A Mettler AE100 electronic analytical balance (Mettler-Toledo International Inc., Greifensee, Zürich, Switzerland) accurate to 0.1 mg was used to measure leaf biomass.

2.3.3. Leaf Disc Feeding Assays with *Hosta*

Leaf disc feeding assays were performed to measure survival, growth, and egg production of *D. reticulatum*. Twenty *D. reticulatum* hatchlings were randomly assigned to each of twelve treatments. Treatments included a romaine lettuce control and either *Hosta* 'Fragrant Blue', *Hosta* 'Guacamole', *Hosta* 'Red October', *Hosta* 'So Sweet', *Hosta* 'Sun Power', or a combination of these cultivars (Table 2.1). These varieties were chosen based on preliminary feeding trials. Newly expanded *Hosta* leaves were used in the feeding assays and feeding was observed on all plant types.

After 21 days development, juvenile slugs were weighed and thereafter weight measurements were taken every third day. The slugs were not weighed on the day they hatched, or throughout the 21 day development period, due to high mortality from excess handling (Thomas, unpublished data). The slugs were weighed on a Mettler AE100 electronic analytical (Mettler-Toledo International Inc., Greifensee, Zürich, Switzerland) balance accurate to 0.1 mg.

Table 2.1. Treatments to study the effect of dietary diversification on survivorship, development, and egg production of *Deroceras reticulatum* (Müller) (Stylommatophora: Agriolimacidae).

Treatment	Diet
1	Romaine Lettuce
2	*Hosta* ‘Fragrant Blue’
3	*Hosta* ‘Guacamole’
4	*Hosta* ‘Red October’
5	*Hosta* ‘So Sweet’
6	*Hosta* ‘Sun Power’
7	*Hosta* ‘Fragrant Blue’ + *Hosta* ‘Red October’
8	*Hosta* ‘Fragrant Blue’ + *Hosta* ‘Sun Power’
9	*Hosta* ‘Red October’ + *Hosta* ‘Sun Power’
10	*Hosta* ‘Fragrant Blue’ + *Hosta* ‘Red October’ + *Hosta* ‘Sun Power’
11	*Hosta* ‘Fragrant Blue’ + *Hosta* ‘Red October’ + *Hosta* ‘So Sweet’
12	*Hosta* ‘Fragrant Blue’ + *Hosta* ‘Red October’ + *Hosta* ‘So Sweet’ + *Hosta* ‘Sun Power’

2.3.4. Leaf Disc Feeding Assays with *Hosta* and Alternative Food Source

In order for the slugs to reach sexual maturity to effectively test fecundity on the different treatments and to increase survival, the above experiment was repeated with an alternative food source of organic romaine lettuce added to each treatment except the cabbage control. An additional control treatment of organic romaine lettuce was also included (Table 2.2). Once slug weight plateaued, indicating completion of the developmental phase of the slug life cycle, a final dry weight was obtained for all surviving slugs to standardize waster. The slugs were dried for 72 hours at 50°C in a Model 280 isotemp vacuum oven. However, due to my miscommunication with an undergraduate laboratory assistant about balance calibration, no useable dry weights were obtained.

Table 2.2. Treatments to study the effect of dietary diversification on survivorship, development, and egg production of *Deroceras reticulatum* (Müller) (Stylommatophora: Agriolimacidae) with romaine lettuce added to each *Hosta* treatment.

Treatment	Diet
1	Romaine Lettuce
2	*Hosta* 'Fragrant Blue'
3	*Hosta* 'Guacamole'
4	*Hosta* 'Red October'
5	*Hosta* 'So Sweet'
6	*Hosta* 'Sun Power'
7	*Hosta* 'Fragrant Blue' + *Hosta* 'Red October'
8	*Hosta* 'Fragrant Blue' + *Hosta* 'Sun Power'
9	*Hosta* 'Red October' + *Hosta* 'Sun Power'
10	*Hosta* 'Fragrant Blue' + *Hosta* 'Red October' + *Hosta* 'Sun Power'
11	*Hosta* 'Fragrant Blue' + *Hosta* 'Red October' + *Hosta* 'So Sweet'
12	*Hosta* 'Fragrant Blue' + *Hosta* 'Red October' + *Hosta* 'So Sweet' + *Hosta* 'Sun Power'
13	Cabbage

2.3.5. Egg Production: Self-fertilization

Slugs are hermaphroditic and have the ability to self-fertilize. Therefore, even though the slugs were kept individually, they had the potential to produce viable offspring. Any eggs produced by slugs in the feeding trials were counted and collected by hand. Egg batches were kept separately in plastic containers (100 mm diameter, 40 mm wide) at 20°C on a 16:8 light:dark cycle until hatching. The floors of the containers were lined with wet cotton (U.S. Cotton Co., Lachine, Québec, Canada) and a 2 cm^2 hole covered with fine mesh provided sufficient air flow to prevent condensation. Egg hatching success, time to hatching, and hatchling weight were recorded.

2.3.6. Statistical Analysis

ANOVA was run on Minitab (Minitab Inc., State College, PA, USA) to compare leaf thickness and toughness and nitrogen, carbon, and water content between plant species and varieties and to test for the effects of treatment on slug development and survival, compare egg production, egg hatching success, and date to hatching. All percentages were arcsine transformed prior to analysis. Means were compared using post hoc Least Significant Differences at $P < 0.05$.

2.4. Results

2.4.1. Plant Characteristics

There were highly significant differences in mean leaf thickness (ANOVA, $F_{6, 63}$ = 86.4, P < 0.001) (Figure 2.1) and mean leaf toughness (ANOVA, $F_{6, 63}$ = 13.0, P < 0.001) (Figure 2.2) between plant types. According to post hoc LSD (P = 0.05), the mean cabbage leaf thickness and toughness were significantly higher than that of romaine lettuce and all *Hosta* varieties. Mean *Hosta* 'Sun Power' leaf thickness was significantly higher than that of *Hosta* 'So Sweet'. Mean *Hosta* 'So Sweet' leaf toughness was significantly lower than that of *Hosta* 'Fragrant Blue' and mean romaine lettuce leaf toughness was significantly lower than that of *Hosta* 'Fragrant Blue,' *Hosta* 'Guacamole', and *Hosta* 'Sun Power'.

There were also highly significant differences in carbon (ANOVA, $F_{6, 63}$ = 26.1, P < 0.001) (Figure 2.3) and nitrogen (ANOVA, $F_{6, 63}$ = 22.6, P < 0.001) (Figure 2.4) content between plant types. According to post hoc LSD (P = 0.05), *Hosta* 'Red October' mean percent carbon content was significantly higher than that of all other plant types, except *Hosta* 'Fragrant Blue'. *Hosta* 'Fragrant Blue' mean percent carbon content was higher than that of *Hosta* 'Sun Power' and romaine lettuce and cabbage mean percent carbon contents were significantly lower than that of all other plant types. *Hosta* 'So Sweet' mean percent nitrogen content was significantly higher than that of all other plant types and cabbage mean percent nitrogen content was significantly lower than that of all other plant types. *Hosta* 'Fragrant Blue' and *Hosta* 'Guacamole' had mean percent nitrogen contents significantly different from all plant types but each other and *Hosta*

‘Red October’, *Hosta* ‘Sun Power’, and romaine lettuce had mean percent nitrogen contents significantly different from all plant types but each other.

Significant differences in mean percent water content were found between plant types (ANOVA, $F_{6, 63} = 24.1$, $P < 0.001$) (Figure 2.5). Post hoc LSD ($P < 0.05$) analysis showed that mean percent water content in lettuce and cabbage were significantly higher than that of all other plant types. *Hosta* ‘Fragrant Blue’ has mean percent water content significantly higher than all other plant types except *Hosta* ‘Red October’ and *Hosta* ‘Sun Power’.

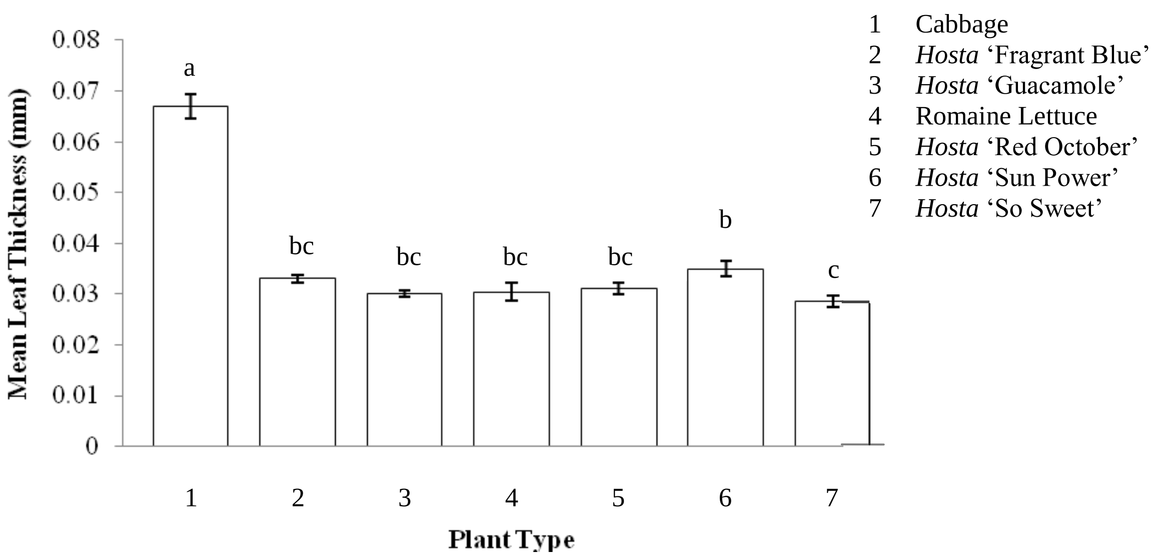

Figure 2.1. Mean leaf thickness (± SE) per *Hosta* variety, romaine lettuce, or cabbage used in dietary diversification study. Letters above bars correspond to statistical differences between treatments.

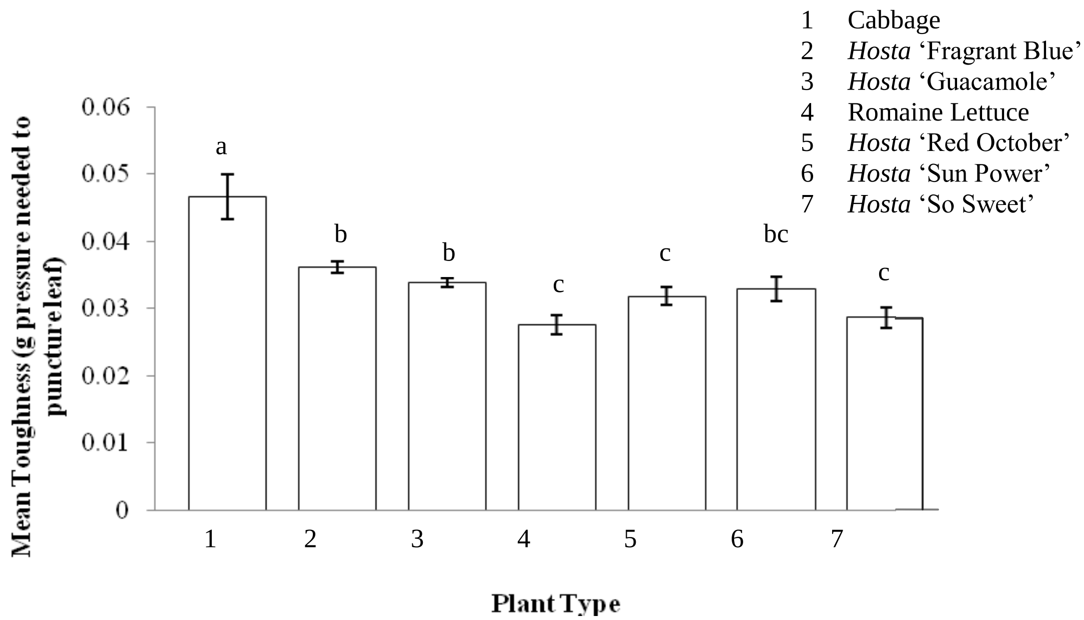

Figure 2.2. Mean leaf toughness (± SE) per *Hosta* variety, romaine lettuce, or cabbage used in dietary diversification study. Letters above bars correspond to statistical differences between treatments.

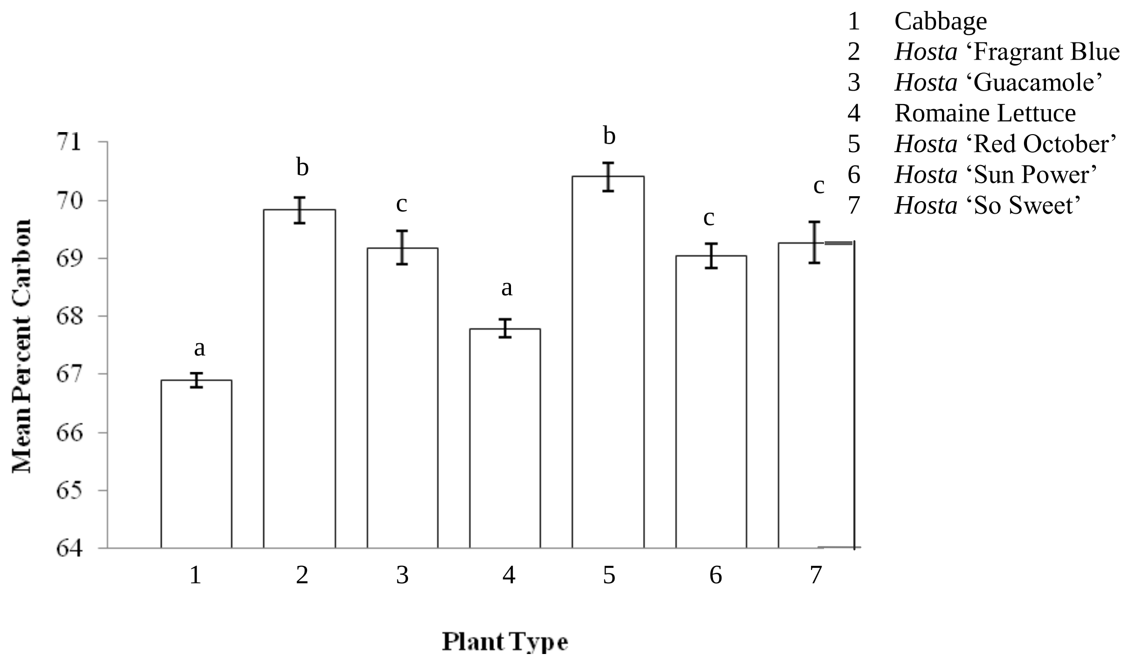

Figure 2.3. Mean percent leaf carbon (± SE) per *Hosta* variety, romaine lettuce, or cabbage used in dietary diversification study. Letters above bars correspond to statistical differences between treatments.

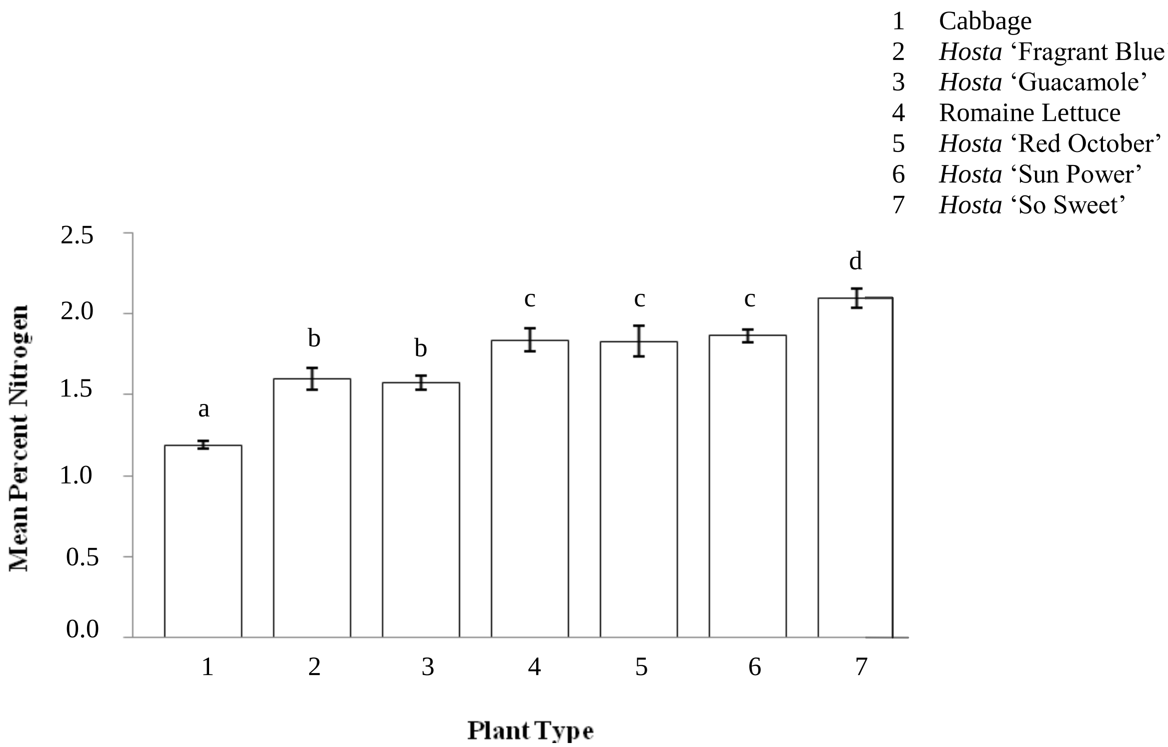

Figure 2.4. Mean percent leaf nitrogen (± SE) per *Hosta* variety, romaine lettuce, or cabbage used in dietary diversification study. Letters above bars correspond to statistical differences between treatments.

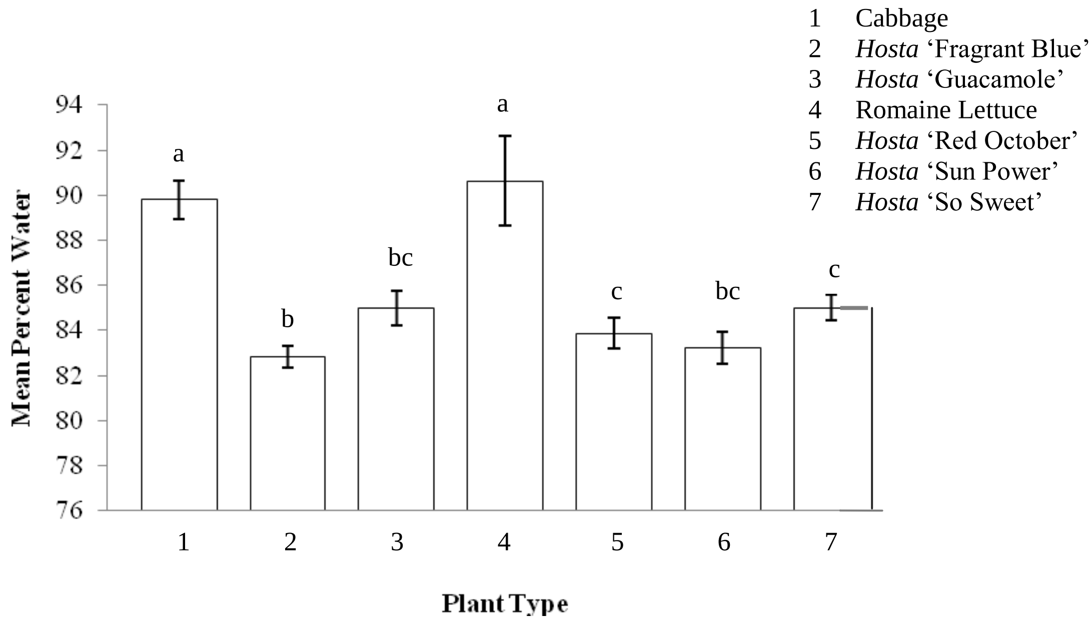

Figure 2.5. Mean percent leaf water content (± SE) per *Hosta* variety, romaine lettuce, or cabbage used in dietary diversification study. Letters above bars correspond to statistical differences between treatments.

2.4.2. Slug Development

In leaf disc feeding assays with treatments containing *Hosta* alone, there were high levels of slug mortality, with slugs from *Hosta* only treatments dying within 102 days of hatching. Slugs fed on the treatment food of romaine lettuce had a significantly greater survival (ANOVA, $F_{11, 197} = 5.6$, $P < 0.001$) compared to *Hosta*-only treatments, with only 3 slugs dying throughout the duration of the study. Therefore, the experiment was repeated with an alternative food source in all *Hosta* treatments in order to increase the percentage of slugs which would development and reach reproductive maturity.

Throughout the leaf disc feeding assay, slug biomass was measured every third day from 21 until 276 days after hatching. The difference between the initial and final slug biomass will be referred to as total Δ slug biomass. The mean difference in total slug biomass was compared between treatments and results were highly significant (ANOVA, $F_{12, 247} = 3.3$, $P < 0.001$) (Figure 2.6) with results observed in the cabbage control treatment significantly different from all other treatments. This treatment (Treatment 13) had the smallest mean total Δ slug biomass with an increase of 336.3 mg. The *Hosta* 'Red October' + *Hosta* 'Sun Power' treatment (Treatment 9) had the greatest mean total Δ slug biomass with an increase of 1420.4 mg; however, there were no significant differences between mean total Δ slug biomass in Treatments 1-12.

The mean difference in biomass per weigh period (every third day) was also compared between treatments and results again showed highly significant differences (ANOVA, $F_{12, 247} = 3.3$, $P < 0.001$), with the mean Δ slug biomass per weigh period in the cabbage control (Treatment 13) significantly different from that of all other treatments. This was also the smallest mean Δ slug biomass per weigh period, with an increase of 4.04 mg. The *Hosta* 'Red October' + *Hosta* 'Sun Power' treatment (Treatment 9) had the largest mean Δ slug biomass per weigh period with an increase of 17.15 mg; however, no significant differences were found between mean Δ slug biomass per weigh period in Treatments 1-12.

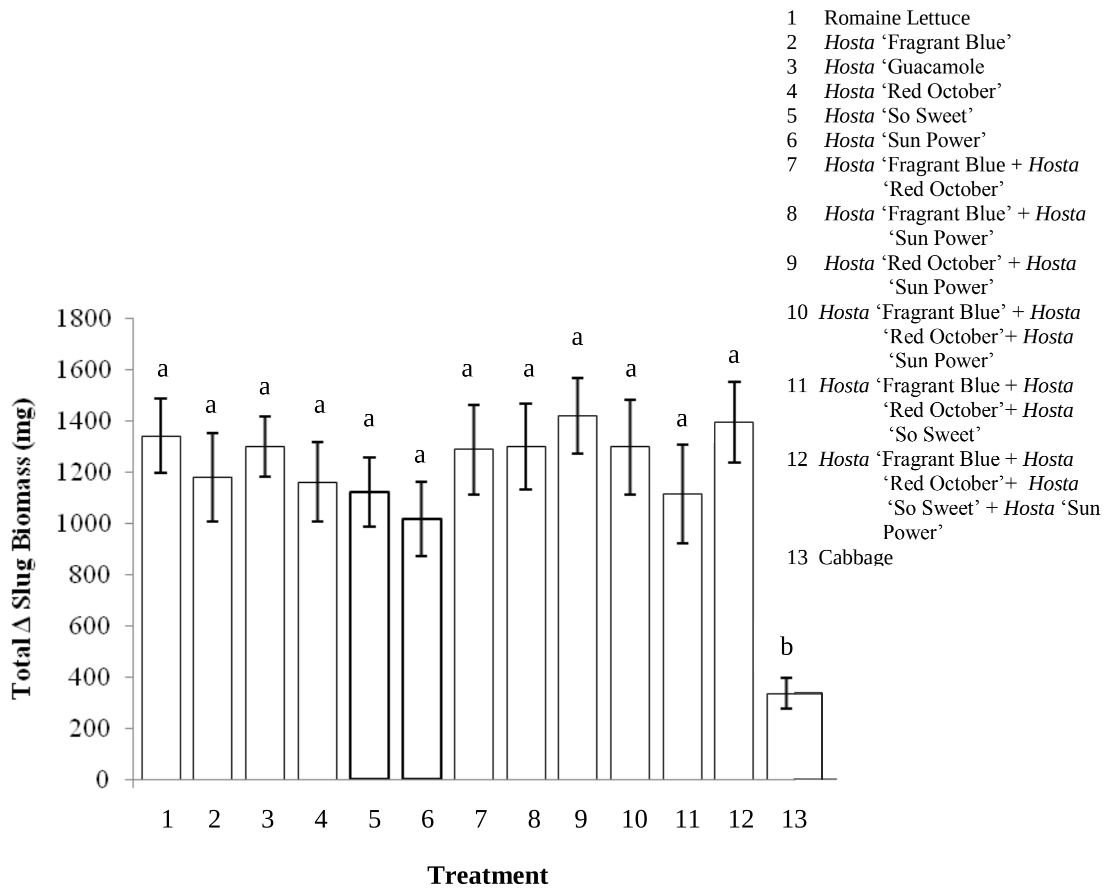

Figure 2.6. Mean total difference between the intitial and final *Deroceras reticulatum* (Müller) (Stylommatophora: Agriolimacidae) biomass (± SE) per treatment food. Letters above bars correspond to statistical differences between treatments.

2.4.3. Egg Production of D. reticulatum

Throughout the study, any *D. reticulatum* eggs found were counted and the number of *D. reticulatum* eggs laid per treatment, eggs hatched per treatment, percent eggs hatched per batch, number of days to hatching, and hatchling biomass were recorded; however, there were no significant differences between treatments for any of these parameters (ANOVA, eggs laid: $F_{11, 228} = 1.2$, $P = 0.29$; eggs hatched: $F_{11, 228}$ =

0.96, $P = 0.48$; percent eggs hatched per batch: $F_{11, 228} = 0.73$, $P = 0.71$; days to hatching: $F_{11, 228} = 1.35$, $P = 0.41$; hatchling biomass: $F_{11, 228} = 0 .51$, $P = 0.81$). No eggs were collected in Treatments 1, 8, and 13 and no eggs hatched in Treatments 2, 3, and 9.

2.5. Discussion

In order to demonstrate the quantitative effects of *Hosta* varities and dietary diversification on the growth, fecundity, and survival of *D. reticulatum*, a feeding assay was conducted using thirteen dietary treatments, ranging in diversity levels from one to four *Hosta* varieties with cabbage and romaine lettuce controls. *Hosta* was chosen for this study, because terrestrial slugs are the most commonly reported pest for this ornamental and *Hosta* is an extremely large genus with several thousand varieties, allowing for differences in plant traits and physical properties which are useful for comparison. The study tested the hypothesis that a diverse diet is beneficial for *D. reticulatum* and allows these herbivores to fulfill their nutritional requirements more effectively than a single-source diet through dietary mixing. Changes in biomass were used to measure the development of the slugs on different diets and leaf characteristics (carbon, nitrogen, and water content, thickness, and toughness) of the plants used in the study were measured to provide a possible explanation for any differences in this development. When the slugs reached sexual maturity and began laying eggs, the number of eggs produced, their hatching success, time to hatching, and hatchling biomass were recorded as an additional measurement of slug developmental differences between treatments.

This research found that there were no significant relationships between dietary diversification and *D. reticulatum* development despite feeding on all varieties, implying the slugs did not benefit from feeding on *Hosta* varieties. The lack of significance between treatments was likely a product of the addition of romaine lettuce to all *Hosta* treatments. This addition was necessary due to high levels of mortality in previous experimentation with *Hosta* varieties in which the only treatment which did not suffer a high level of mortality was the romaine lettuce control. The only treatment in this study showing significantly different mean total Δ slug biomass was the cabbage control. This is the only treatment in which no romaine lettuce was added, which supports the hypothesis that the uniformity of slug development was caused by the addition of romaine lettuce to all other treatments, because it was a preferred food source for the animals. The significantly lower level of development on organic cabbage was not expected. Cabbage is a member of the family Brassicaceae, which includes, but is not limited to, broccoli (*Brassica oleracea* var. *italic* Linnaeus), brussels sprouts (*Brassica oleracea* var. *gemmifera* Linnaeus), cauliflower (*Brassica oleracea* var. *botrytis* Linnaeus), kale (*Brassica oleracea* var. *acephala* Linnaeus), turnip (*Brassica rapa* var. *rapa* Linnaeus), rapeseed (*Brassica rapalnapus* var. *oleifera* Linnaeus), mustard (*Brassica juncea* Linnaeus), radish (*Raphanus sativus* Linnaeus), and watercress (*Nasturtium officinale* Linnaeus) (Koch *et al*. 2003). Slug feeding on cabbage and other *Brassica sp*. has previously been recorded (Barnes and Weil 1945, Anonymous 1979) and therefore *D. reticulatum* feeding was expected in this study. However, levels of such feeding on brassica have never been quantified. Observations made throughout the experiment showed very little feeding on cabbage and therefore, this may be due to physical or chemical characteristics making the plant unpalatable to *D. reticulatum.*

Mean cabbage leaf thickness and toughness were significantly higher than that of romaine lettuce and all *Hosta* varieties. While the mean percent carbon and water content of cabbage was significantly lower than that of all *Hosta* varieties, it is unlikely that these factors alone affected palatability and/or slug development. The mean percent carbon and water content of romaine lettuce, the plant most likely responsible for the high level of survival and lack of significance in *D. reticulatum* development in this study, was not significantly different from that of cabbage and yet, slug development was significantly different on these two plant types. Lower mean percent nitrogen content may account for the low levels of slug development on cabbage, since high levels of nitrogen have been demonstrated to increase survival and abundance of young herbivores (White 1984). However, *Hosta* 'So Sweet' mean percent nitrogen content was significantly higher than that of all other plant types and development on this plant was not significantly higher than the other plant types. Members of the family Brassicaceae, of which cabbage is one, are known for production of anti-herbivorous secondary chemicals such as glucosinolates, or mustard oils (Vašák 2002), which are known to be feeding deterrents for slugs (Buschmann *et al*. 2006). Plants in this family have also been recorded exhibiting hypersensitivity reaction (HR) in which a necrotic zone appears on a plant around pathogens or pest eggs to isolate the infected area and protect the rest of the plant (Shapiro and DeVay 1987). However, several Brassicaceae species are highly palatable to slugs and some slug species have even shown a preference for Brassicaceae over other families (Rees and Brown 1992, Briner and Frank 1998). It is likely a combination of significantly higher plant thickness and toughness in combination with the chemical composition of cabbage that significantly reduced slug development and/or palatability on this brassica species.

Hosta varieties are most often classified based on color: blue, gold, green, and variegated. It has commonly been asserted that the *Hosta* varieties most susceptible to damage by terrestrial slugs are those with thin leaves and those with leaves growing close to the ground (for this study, the height of the *Hosta* was immaterial as slugs were fed leaf discs). In this experiment, five *Hosta* varieties (one gold, one green, one blue, and two variegated) were tested not only to determine the effect dietary diversification had on terrestrial slug development, but also to quantify differences in leaf characteristics that may elucidate why some *Hosta* varieties seem to be more susceptible than others to slug damage. The varieties chosen were all listed as some of the most popular varieties in North America and several were lauded as slug resistant. Observations showed that the most palatable *Hosta* varieties were *Hosta* ‘Red October’ (a green variety) and *Hosta* ‘Guacamole’ (a variegated variety). Observations also showed that the least palatable *Hosta* variety was ‘Fragrant Blue’ (a blue variety), which was expected. According to *Hosta* growers, blue varieties are the most slug resistant. Growers believe this is due to the waxy coating on the leaves of blue *Hosta* varieties that gives these plants their blue tint; however, this has never been tested scientifically. Unfortunately, without significant differences between *Hosta* varieties, nutritional comparisons were inconclusive.

These results clearly demonstrate the need for additional research into the nutritional requirements of pestiferous terrestrial slugs in order to determine the effect a diverse diet has on slug development and to serve as a database to evaluate the nutritional value of different *Hosta* varieties. Also, more *Hosta* varieties in each color group should be evaluated in order to make generalizations as to the nutritional qualities of the different groups. Finally, feeding preference experiments are necessary to definitively show that *D. reticulatum* would seek out certain varieties over others. Researchers should also conduct field experiments with planted *Hosta* in addition to leaf disc feeding assays as assays may skew results in favor of greater herbivory by removing physical barriers such as tough leaf edges or by releasing chemicals that attract herbivores or by simply putting an animal in artificial conditions. This further research is necessary to assist *Hosta* growers and gardeners in choosing varieties which are the best investments.

Chapter Three: Effect of dietary diversification on self-fertilization *versus* outcrossing in the non-native mollusk, *Deroceras reticulatum* (Müller)

3.1. Summary

All terrestrial slugs are hermaphroditic (South 1992) and several slug species are capable of self-fertilization, which may facilitate colonization of new areas, often with negative economic and environmental consequences. Experiments have shown that many gastropods reproduce predominately by self-fertilization or outcrossing (Jordaens *et al*. 2000). Research into the life history of *D. reticulatum* found that while this species has the ability to self-fertilize, it is a predominately outcrossing species (Nicholas 1984) and Nicklas and Hoffman (1981) theorized that *D. reticulatum* was an obligate outcrossing species. This study compared the self-fertilizing *versus* outcrossing reproductive capabilities and proclivities of this species and tested the effect that dietary diversification has on egg production and viability with these reproductive methods in order to analyze the invasive capabilities of this non-native gastropod in North America. While some *D. reticulatum* were kept in isolation, others were kept in breeding pairs and the number of eggs produced, percent hatching, and time to hatching were recorded. This tested the hypotheses that a greater number of viable *D. reticulatum* eggs would be produced in pairs with the potential for outcrossing and that egg production and viability would increase with dietary diversification. Results showed no significant correlation between dietary diversification and fecundity. However, there were significant differences between fecundity and the potential methods of reproduction. Egg production was significantly greater in treatments in which slugs were kept individually than in treatments in which slugs had the potential to outcross. This data does not support

previous research stating that *D. reticulatum* is a predominately, if not obligatory outcrossing species, which may be advantageous for this species by allowing for high individual fecundity in periods of isolation. This would increase its threat as a biological invader.

3.2. Introduction

While all terrestrial slugs are hermaphroditic, containing both male and female sexual organs (South 1992), there is inter- and intra-specific variation in the reproductive systems of these animals. The interspecific variation is useful for species identification; however, as is often the case, intraspecific variation makes it difficult to generalize species characteristics and behaviors. For example, some *D. laeve* individuals are aphallic, while others are euphallic with both forms occurring together at the same location in different seasons (Quick 1960) and this has led to questions relating to the hermaphroditic status of this species. Instead they hypothesized that *D. laeve* had both protogynous and hermaphroditic forms (Lupu 1977). It has even been hypothesized that this species procreates by parthenogenesis (Nicklas and Hoffman 1981, Hoffman 1983). This is just one example of the complexities of the reproductive systems and strategies of terrestrial slugs.

Several slug species are capable of self-fertilization, including those in the genera *Philomycus* and *Ariolimax,* Arionid species, *Limax cinereoniger* Wolf*, M. gagates*, *Vaginulus borellianus* (Colosi) (Stylommatophora: Veronicellidae), and *Laevicaulis alte* (Férrusac) (Stylommatophora: Veronicellidae) with multiple generations of the latter three species maintained through self-fertilization (Duncan 1975). Research into the reproductive behavior of *A. hortensis* and *D. reticulatum* found that while both species have the ability to self-fertilize, only *A. hortensis* does this regularly when isolated. In this study, *D. reticulatum* laid eggs in isolation; however, many of these batches were not viable, implying egg production was independent of mating and fertilization (Nicholas 1984). South (1982) also reported that *D. reticulatum* frequently laid infertile egg batches when isolated and Runham and Hunter (1970) stated that this species rarely self-fertilizes. Nicklas and Hoffman (1981) theorized that *D. reticulatum* was an obligate outcrossing species. *Deroceras* species known to self-fertilize more frequently than *D. reticulatum* are *D. agreste* (Luther 1915, Maury and Reygrobellet 1963), which produced multiple generations per year (Chen *et al*. 1984), *D. laeve*, and *Deroceras meridionale* Reygrobellet (Maury and Reygrobellet 1963). Individuals in these species may be more isolated than predominately outcrossing species and it may therefore be advantageous for them to readily self-fertilize.

Experiments have shown that many gastropods reproduce by predominately self-fertilizing or outcrossing (Jordaens *et al*. 2000). Through gel electrophoresis studying the genetic variation in eastern North American slugs, McCracken and Selander (1980) were able to label slugs based on their likely mode of reproduction. Species that were monogenic were likely self-fertile, whereas species that showed high levels of heterozygosity likely bred through outcrossing. According to this study, species in which facultative or obligatory self-fertilization is the normal behavior are *A. circumscriptus*, *Arion fasciatus s.s.* (Nilsson), *A. intermedius*, *Arion silvaticus* (Lohmander), and two out of the three subspecies of *A. subfuscus* (McCracken and Selander 1980). However, a study by Jordaens *et al.* (2000) showed a high level of heterozygosity in central European *A. fasciatus*, implying some degree of outcrossing.

In a moist, cool climate if there is another slug present, several species are more likely to choose that option. These include *A. hortensis s.s.*, *D. reticulatum*, *Lehmannia valentiana* (Ferussac), *L. maximus*, and *Philomycus carolinianus* (Bosc), the third strain of *A. subfuscus*, and three other species of *Philomycus* (McCracken and Selander 1980). Other species that seem to choose outcrossing are *Arion distinctus* (Mabille), *Arion lusitanicus* (Mabille), and *Arion owenii* (Davies). After several surveys in the British Isles having similar results, it was concluded that breeding systems of terrestrial slugs were not modified through the colonization of North America and that self-fertilizing European species were especially well adapted to colonizing this continent (Foltz *et al*. 1982).

There are many studies showing that the development and fecundity of polyphagous herbivores are affected by diet and dietary diversification (Sonoda *et al*. 1991, Moreau *et al.* 2006, Amaresekare *et al.* 2008, Unsicker *et al*. 2008, Wang *et al*. 2008); however, there has been very little research examining the role a diverse diet plays in the life history and fecundity of terrestrial slugs. These animals are generalists and therefore eat a wide variety of foods including healthy and decaying plant material, fungi, algae, lichens, moss, flesh, feces, bones, bread products, corn products, old tea leaves, and coffee grounds (Barnes and Weil 1945). The objective of this study was to demonstrate the quantitative effects of treatment food and dietary diversification on the fecundity of *D. reticulatum* in individual (self-fertilizing) and paired (outcrossing) experimental conditions. It tested the hypothesis that egg production and viability would increase and time to hatching would decrease when slugs had the opportunity to outcross. It also tested the hypothesis that fecundity would increase in treatments with greater dietary diversification since it would allow these generalist feeders to fulfill their nutritional requirements more effectively than a single-source diet through dietary mixing. This hypothesis was tested by feeding adult slugs a diet ranging in diversity levels from one to two *Hosta* varieties (with romaine lettuce added to all treatments to increase survival and accurately test fecundity). Leaf characteristics (carbon, nitrogen, and water content, as well as thickness and toughness) of romaine lettuce and *Hosta* varieties were measured to provide a possible explanation for any differences in slug fecundity. The number of eggs produced, their hatching success, and time to hatching were used to measure fecundity.

3.3. Materials and Methods

3.3.1. Slug Collection and Maintenance

D. reticulatum were collected from the Horticultural Research Farm of the University of Kentucky (37°58’N 84°32’W) and the University of Kentucky Spindletop Research Farm (38°07’N 84°30’W), both located in Lexington, Fayette County, Kentucky. Slugs were maintained in plastic containers (100 mm in diameter and 40 mm wide) at 20°C on a 16:8 light:dark cycle with five slugs per container. They were fed an *ad libitum* supply of fresh organic cabbage, romaine lettuce, carrot, and potato. The floors of the containers were lined with wet cotton (U.S. Cotton Co., Lachine, Québec, Canada) and six small air holes created by inserted sharp forceps into side of the plastic container provided sufficient ventilation for the health of the animals. The slugs were standardized to laboratory conditions for one week.

3.3.2. Measurement of Plant Characteristics

Plant traits were measured to quantify differences in leaf characteristics of romaine lettuce, *Hosta* ‘Red October’, and *Hosta* ‘So Sweet’. Refer to Chapter 2 for *Hosta* care and measurement protocols.

3.3.3. Self-fertilization *vs*. Outcrossing in *D. reticulatum*

Following lab conditioning, each slug was weighed on a Mettler AE100 electronic analytical balance accurate to 0.1 mg, randomly assigned to one of the treatments listed in Table 3.1, and fed an *ad libitum* supply of treatment food. There were no significant differences in slug biomass between treatments (ANOVA, $F_{7, 72} = 0.94$, $P = 0.482$) at the start of the experiments. There were ten replications per treatment. In order to effectively test fecundity on the different treatments and in order to decrease mortality, organic romaine lettuce was included in each *Hosta* treatment. Slugs in self-fertilization treatments were kept individually, while slugs in outcrossing treatments were kept in breeding pairs. Eggs produced were counted and collected by hand. Egg batches were kept separately in plastic containers as detailed above. Instead of the six small holes in the containers of the adult slugs, a hole measuring 2 cm^2 covered with fine mesh provided sufficient ventilation to prevent condensation and emigration of hatchlings. Egg production, egg hatching success, and time to hatching were recorded. The experiment continued for one month.

Table 3.1. Treatments to study egg production of *Deroceras reticulatum* (Müller) (Stylommatophora: Agriolimacidae) self-fertilizing and outcrossing on different diets with romaine lettuce added to each treatment to effectively test fecundity and increase survival.

Treatment	Diet
1	Romaine Lettuce individual
2	Romaine Lettuce paired
3	*Hosta* 'Red October' individual
4	*Hosta* 'Red October' paired
5	*Hosta* 'So Sweet' individual
6	*Hosta* 'So Sweet' paired
7	*Hosta* 'Red October' + *Hosta* 'So Sweet' individual
8	*Hosta* 'Red October' + *Hosta* 'So Sweet' paired

3.3.4. Statistical Analysis

ANOVA was run on Minitab (Minitab Inc., State College, PA, USA) to compare mean leaf thickness and toughness and mean nitrogen, carbon, and water content between treatments, to compare mean initial slug biomass across treatments (weights of slug pairs in sexual treatments averaged), and to test for the effects of treatment on mean egg production, mean egg hatching success (treatment and batch), and mean time to hatching. All percentages were arcsine transformed prior to analysis. Means were compared using post hoc Least Significant Differences for $P < 0.05$.

3.4. Results

3.4.1. Plant characteristics

There were no significant differences in mean leaf thickness (ANOVA, $F_{2, 27}$ = 1.01, P = 0.377) and mean leaf toughness (ANOVA, $F_{2, 27}$ = 2.30, P = 0.120) between plant types used in this study (previously presented in figures 2.1 and 2.2). However, there were highly significant differences in carbon (ANOVA, $F_{2, 27}$ = 25.61, P < 0.001) (Figure 2.3) and nitrogen (ANOVA, $F_{2, 27}$ = 4.05, P = 0.029) (Figure 2.4) content between plant types, with the mean percentage of carbon in *Hosta* 'Red October' being significantly higher (70.4 %) than all of the other plant types and romaine lettuce (67.8 %) mean percent carbon content being significantly lower than all of the other plant types. *Hosta* 'So Sweet' mean percent nitrogen content (20.9 %) was significantly higher than that of all other plant types. Mean percent nitrogen contents of *Hosta* 'Red October' (18.3 %) and romaine lettuce (18.4 %) were not significantly different from each other. There were also significant differences in mean percent water content between plant types (ANOVA, $F_{2, 27}$ = 21.18, P < 0.001) (Figure 2.5) with mean percent water content in lettuce (90.6 %) significantly higher than that of all other plant types.

3.4.2. Self-fertilization *vs*. Outcrossing in *D. reticulatum*

Eggs were collected from all treatments and egg production, egg hatching success, and time to hatching were recorded and analyzed by treatment. Results showed a significant difference in mean number of eggs laid per slug between treatments (ANOVA, $F_{7, 72}$ = 2.14, P = 0.05) (Figure 3.1). Post hoc LSD (P = 0.05) analysis showed that the mean number of eggs laid by slugs in Treatments 2 (99.6) and 6 (104.95) were significantly lower than those laid by slugs in Treatments 1 (191.9), 3 (158.3), and 7 (184.7). The mean number of eggs laid by slugs in Treatment 4 (131.75) were significantly fewer than those laid by slugs in Treatments 1 and 7 and the number of eggs laid by slugs in Treatment 8 were significantly fewer than those laid by slugs in Treatment 1. The mean number of eggs laid by slugs in Treatment 5 were not significantly different than those laid in any other treatment. However, there were no significant differences in percent eggs hatched per batch (ANOVA, $F_{7, 72} = 0.98$, $P = 0.453$), percent eggs hatched per treatment (ANOVA, $F_{7, 72} = 0.87$, $P = 0.532$), and days to hatching (ANOVA, $F_{7, 72} = 2.01$, $P = 0.065$).

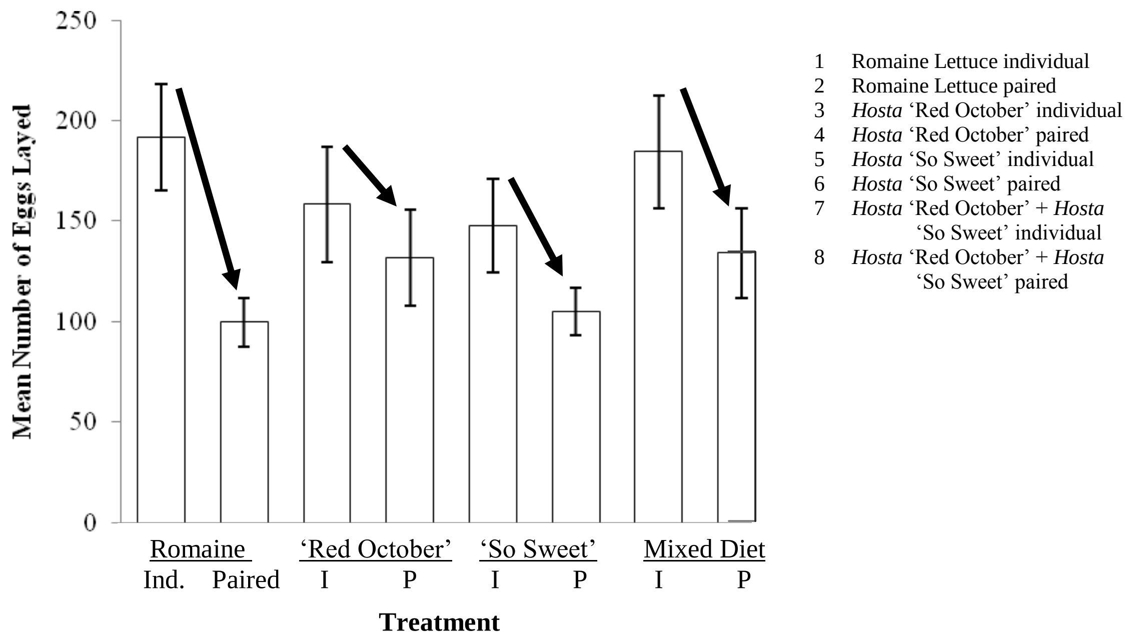

Figure 3.1. Mean number (± S.E.) of *Deroceras reticulatum* (Müller) (Stylommatophora: Agriolimacidae) eggs laid per slug per treatment. The eight treatments were divided into 4 diets with an individually kept slug (self-fertilizing treatment) or a pair of slugs (outcrossing treatment) per treatment.

3.5. Discussion

Hermaphroditic organisms are excellent study organisms for the study of reproductive methods, such as selfing *versus* outcrossing, and examine the role that diet plays in these complicated and interesting reproductive systems (Jordaens *et al.* 2000). Since terrestrial slugs are hermaphroditic, most species have the opportunity to self-fertilize when conditions for sexual reproduction are unfavorable. However, many slug species can almost always only self-fertilize or outcross (Jordaens *et al.* 2000). In this study I compared the reproductive capacity between *D. reticulatum* individuals that were kept in reproductive isolation and therefore had to self-fertilize to produce viable eggs and individuals that were kept in pairs and therefore had the opportunity to either self-fertilize or outcross. As prior research has shown this species to be a predominately outcrossing species, the hypothesis tested was that egg production and viability of eggs would increase and time to hatching would decrease when slugs had the opportunity to outcross. The hypothesis that fecundity would increase in treatments with greater dietary diversification since it would allow these generalist feeders to fulfill their nutritional requirements more effectively than a single-source diet through dietary mixing was also tested. This hypothesis was tested by feeding adult slugs a diet ranging in diversity levels from one to two *Hosta* varieties (with romaine lettuce added to all treatments to increase survival and accurately test fecundity).

There were no significant differences based on dietary diversification in this study; however, this may be due to the similarities between plant species. Additionally, potential significant results may have been negated by the addition of romaine lettuce to every treatment. However, results did show a significant difference in mean egg production (per slug) between slugs in self-fertilizing and outcrossing treatments, with species in self-fertilizing treatments consistently producing more eggs than those in the outcrossing treatments, regardless of treatment food. This research alone does not contradict previous studies, stating that *D. reticulatum* was a primarily outcrossing species, producing unfertilized egg batches when kept in isolation, which implied that the ability to produce eggs was independent of mating and fertilization (Nicholas 1984). However, when mean egg hatching success was compared, there were no significant differences between treatments. Eggs laid by isolated and therefore self-fertilizing slugs were just as viable as eggs laid by slugs in breeding pairs who had had the opportunity to outcross. (Runham and Hunter 1970, South 1982, Nicholas 1984). In fact, Nicklas and Hoffman (1981) hypothesized that this *D. reticulatum* is an obligate outcrossing species. The slugs in this study reproduced at the expected rate as all mean values for egg production fell within the accepted value of egg production by *D. reticulatum,* which is up to 500 eggs per year (Carrick 1938).

Results in this study support research conducted on other *Deroceras* species. Chen *et al*. (1984) found that fecundity by self-fertilization in *D. agreste* could be two to four times higher than by outcrossing. They also found the growth rate of the young produced through self-fertilization was higher and that these slugs lived longer than young produced through traditional mating behavior. Comparisons of the growth and development of F1 *D. reticulatum* slugs produced through self-fertilizing and outcrossing would be beneficial in gaining a greater understanding of the reproductive nature of this species. Further research is also necessary to test for the effects of self-fertilization and outcrossing on the fitness of self-fertilizing *versus* outcrossing slugs *i.e.* a comparison of the number of viable F2 offspring.

Research into the reproductive status of non-native slugs is necessary in order to assess the threat level of these species and prioritize control measures. Self-fertilization would be beneficial to invasions by non-native gastropods (Foltz *et al*. 1982) by accelerating population growth. An isolated slug carried into North America on a plant from Europe with a proclivity for self-fertilization would have the capability to reproduce shortly after arrival if not *en route*. This would have large negative effects on American agricultural, horticultural, and floricultural industries as each individual slug has the ability to start a population in a new area. Therefore, the control of those species likely to self-fertilize should be given priority over those that require a mate to produce viable offspring. Two slug pests already present in Kentucky have been shown to favor inbreeding: *A. intermedius* and two strains of *A. subfuscus* (McCracken and Selander 1980). This study has shown that a third pest species in the state may favor self-fertilization, making the implementation of efficient management techniques even more urgent.

Chapter Four: Population regulation of non-native slugs by carabid beetles: effects of density and diversity of prey resources on biological control

4.1. Summary

The infiltrations into North America by non-native gastropods are becoming more common and are of concern to regulatory agencies, agriculturalists, and conservation organizations. These animals have the potential to impact crop yield in agriculture, reduce the aesthetic value of horticultural crops and influence food web structure through the displacement of native species. However, native predators may serve as a highly effective method of control for these non-native slugs and could substantially reduce the non-target risks involved with classical biological control programs. In this study, the biological control capacity of an abundant native North American predator, *S. quadriceps*, against populations of the non-native slug, *D. reticulatum*, was quantified, and its effect on plant growth and development evaluated by measuring damage inflicted to young *Hosta* plants. Importantly, given that *S. quadriceps* is a generalist predator, this study also investigated whether increased levels of dietary diversification influenced the slug – carabid trophic pathway, thereby leading to an increased level of plant feeding by *D. reticulatum* in plots with high density and diversity of alternative prey. The greatest level of damage to *Hosta* plants, calculated as the percent of leaf area lost during the experiment, occurred in treatments containing slugs without carabid beetles, indicating some suppression of pest populations occurred. Interestingly, no significant difference in percent leaf area loss was observed when an alternative food source was available for the carabid beetles. These results indicate that *S. quadriceps* may be an effective conservation biological control agent for use against non-native gastropod species in

North America and that the availability of alternative prey does not diminish the predatory capacity of this beetle.

4.2. Introduction

Due to increases in global trade and international trade agreements that promote the rapid movement of cargo around the world, biological invasions by non-native gastropods into North America are becoming more common. Such introductions are of concern to regulatory agencies, agriculturalists, and conservation organizations. Robinson (1999) listed 4,900 gastropods intercepted in shipments entering the United States from 100 countries between 1993 and 1998 and there are currently over eighty established non-native slug and snail species in the United States and Canada (Mc Donnell *et al*. 2008). Little is known regarding the impact of non-native slugs in North America; however, in Great Britain in 1985, these pests caused losses of $14 million and $5 million respectively to potato and winter wheat crops alone (Port and Port 1986). Financially, the potential of these animals to induce significant yield loss is high, considering they feed on commodities as diverse as cabbage, wheat, alfalfa, corn, soybean, brassicas, carrots, celery, strawberries, cucumbers, chicory, and runner, broad, and French beans (South 1992). Most damage occurs at the seedling stage (South 1992) although with favorable climatic conditions, slugs can impact crops throughout the growing cycle. These pests also feed heavily on flowering plants and ornamentals (Eaton and Tomsett 1976, South 1992), including *Hosta* (Asparagales: Agavaceae) plants, the most commonly planted perennial in the United States (Why Hostas?, www.hostahosta.com/whyhostas.html). This genus consists of sixty-seven species (Hosta

Species Update, www.hostalibrary.org/species/index.html) of herbaceous plants native to northeast Asia. They are generally shade-tolerant plants with broad leaves that grow from corms or rhizomes, and are extremely hardy and robust ornamentals that have very few pests, making them popular in the urban environment. The only herbivores known to frequently feed on these plants are deer and gastropods and their favored planting habitats (shady and damp areas) make them highly vulnerable to the latter species.

Many slugs are very common pests in residential gardens. Barnes and Weil (1944, 1945) performed a survey of fifty gardens in Hertfordshire, United Kingdom, and found that *D. reticulatum* were found in every garden on every sampling date with 3 to 185 slugs collected on or close to the soil surface in just 30 minutes of searching. Such high numbers clearly demonstrate the potential for significant plant damage to occur, increasing the need for control options (chemical or biological) to be considered by homeowners (discussed in detail in Chapter 1).

The long list of non-native slugs in Kentucky includes many species with a known feeding ecology and pest status reported throughout much of Europe, including *A. intermedius*, *D. reticulatum*, and *L. maximus.* The presence of these, and other, species therefore poses a threat to the state's agricultural revenue given the high yield losses that are frequently reported. In 2005, Kentucky's cash receipts for corn exceeded $336 million, soybeans $319 million, wheat $66 million, apples $2 million, peaches $650 thousand, while other fruits, nuts, and berries totaled over $3 million. In addition, the cash receipts for vegetables totaled $19 million and the floricultural industry generated over $43 million in revenue (USDA – NASS Kentucky Field Office 2006). As previously documented, these are all important food sources for slug pests (South 1992) and during favorable weather patterns are at risk from slug damage, particularly since there is a very low damage threshold on many of these commodities.

Farmers and gardeners use a variety of methods to control slug damage including beer traps, copper barriers, and salt (Gordon 1994), diatomaceous earth, molluskicides, as well as alternative food sources such as chickweed (*Stellaria media* Linnaeus) (Caryophyllales: Caryophyllaceae), dandelion (*Taraxacum officinale* Weber) (Asterales: Asteraceae), and wild white clover (*Trifolium repens* Linnaeus) (Fabales: Fabaceae), among many other plants (Cook *et al.* 1996). However, since chemical control often leads to adverse effects on non-target organisms and is, for the most part, an unsustainable method of control, integrated pest management is often a favored alternative for slug control (Cook *et al*. 1996). The use of natural enemies, such as ground beetles (Coleoptera: Carabidae), to mitigate the effects of non-native mollusks to the agricultural or urban environment and thus reduce the need for chemical methods of control has been of interest due to the widely documented non-target effects associated with pesticide use and its storage, as well as the inconvenience or ineffectiveness of some of the other methods of control. Implementation of biological control practices by Master Gardeners can significantly reduce the quantities of pesticides applied in urban and suburban gardens (Sadof *et al*. 2004).

An alternative approach to using native species for pest control is classical biological control, the means by which a pest is regulated or controlled by importing natural enemies from its host range. Such forms of control have been highly successful in applications against a wide range of taxonomically diverse pests, including insects, mites and weed species (reviewed by Hajek *et al*. 2007). Some traits that an effective classical biological control agent should have are 1) narrow prey specificity, 2) high prey-searching efficiency, and 3) the ability to increase population size quickly (Caltagirone 1989). However, due to the widely reported risks of classic biological control, the importation of biological control agents are extensively researched before a classical biological control program is enacted.

Therefore, the use of native predators and/or parasitoids may substantially reduce the non-target risks involved in importing natural enemies to control invasive species (Symondson *et al.* 2002b). For example, native predators and parasitoids have been shown to be effective biological control agents of *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) in California alfalfa (Ehler 2007) while the generalist predator *Orius insidiosus* (Say) (Hemiptera: Anthocoridae) has been demonstrated as having considerable potential in regulating soybean aphid densities early in the year (Harwood *et al.* 2007). It is therefore essential that native species are carefully and accurately identified as a potential means for controlling invasive pest populations, including slugs, in North America.

Carabid beetles are important invertebrate natural enemies of slugs, both above and below the soil surface (Davies 1953, Mead 1961, Stephenson and Knutson 1966, Tod 1970, Cornic 1973, Tod 1973, Baronio 1974, Mead 1979, Symondson *et al.* 1996, 2000, McKemey *et al.* 2001, Paill *et al.* 2002, Symondson 2002a, 2002b, Oberholzer *et al.* 2003, Chabert and Beaufreton 2004, Chabert and Gandrey 2004, Choi *et al.* 2004, Dodd *et al.* 2004, Foltan *et al.* 2004, King *et al.* 2004). Additionally, there are over 40,000 species of carabid beetles worldwide (Wiedenmann *et al.* 2004), including regions where non-native slugs pose a risk for agricultural and horticultural production. These generalist predators have been shown to feed on slugs in the laboratory (McKemey *et al*. 2001, Oberholzer *et al.* 2003) and in the field (Symondson *et al.* 1996, 2002a, Traugott 2003). In one field experiment, approximately 84% of the carabids *Pterostichus melanarius* (Illiger) (Coleoptera: Carabidae) collected from an arable ecosystem were found to contain slug remains (Symondson *et al.* 1996) and these beetles appear to show aggregative responses, locating to areas of high slug density (Bohan *et al.* 2000). Carabid beetles have also been shown to feed on slugs of all size classes (McKemey *et al.* 2001), as well as eggs on or below the soil surface, and they are extremely common in both home gardens in urban/suburban environments (Wiedenmann *et al.* 2004) and a variety of agricultural commodities (e.g., Wiedenmann *et al*. 1992, Elliott *et al*. 2006, Hatten *et al.* 2007). Additional evidence that carabid beetles are major predators of slugs has been indirectly demonstrated by examination of slug behavior in the presence of these natural enemies. Slugs are capable of detecting chemicals found in carabid feces or chemicals that the predators use for communication, providing a warning mechanism to enable an escape response. The fact that slugs display this behavioral response to carabid beetles further shows the interrelated nature of the two organisms (Armsworth *et al*. 2005).

Given this potential for slug control by carabid beetles, the objective of this study was to quantify the biological control capacity of a key native North American generalist predator, *S. quadriceps*, against non-native slug populations and the subsequent effect on plant growth and development. This experiment compared herbivory on young *Hosta* plants by the non-native slug *D. reticulatum* and the effect of *S. quadriceps* on levels of plant damage and tested the hypothesis that the presence of carabid beetles will significantly reduce slug herbivory on plants. Furthermore, given that *S. quadriceps* is a generalist predator and alternative prey often divert predators from feeding on target pests in the field (Harwood *et al*. 2004) and reduce pest suppression in the laboratory (Symondson *et al*. 2006), the hypothesis that dietary diversification in predators will disrupt the slug – carabid trophic pathway and lead to an increase in plant damage, was examined.

4.3. Materials and Methods

4.3.1. Slug Collection and Maintenance

D. reticulatum were reared in the laboratory in plastic containers (100 mm in diameter and 40 mm wide) at 20°C on a 16:8 light:dark cycle. The base of the containers were lined with wet cotton (U.S. Cotton Co., Lachine, Québec, Canada) and a hole on the side of the container measuring 2 cm^2 covered with fine mesh to prevent slugs from exiting the container provided sufficient ventilation to minimize condensation. Laboratory populations of *D. reticulatum* were initially established from collections in fields of alfalfa and corn at the University of Kentucky Spindletop Research Station in Fayette County, Kentucky (GPS Coordinates: 38°07'N, 84°30'W) and from strawberry fields at the Horticultural Research Farm in Fayette County, Kentucky (GPS: 37°58'N, 84°32'W). Slugs were maintained in groups of five individuals per plastic containers, as described above, to minimize the risk of nematode and disease transmission between field-collected individuals. They were provided with an *ad libitum* supply of fresh organic cabbage, romaine lettuce, carrot, and potato.

4.3.2. Beetle Collection and Maintenance

Live female *S. quadriceps* were collected from dry pitfall traps that were inspected every morning and under refuge traps in fields of alfalfa and corn at the University of Kentucky Spindletop Research Station in Fayette County, Kentucky. Specimens were also collected under refuge traps in strawberry fields at the Horticultural

Research Farm in Fayette County, Kentucky. Following collection, beetles were maintained at 16 °C on a 16:8 L:D cycle and kept individually in plastic containers (diameter 100 mm, depth 40 mm) with approximately 20 mm of organic peat mix (Millburn Peat Company, Inc., La Porte, IN, USA) covering the floor of the containers. The peat was examined every third day and remoistened if necessary. Prior to the experiment, *S. quadriceps* were provided an *ad libitum* diet of *Musca domestica* (Linnaeus) (Diptera: Muscidae) pupae (Oregon Feeder Insects, Inc., Tillamook, OR, USA). Any uneaten pupae were removed every third day, when the moisture level was examined, and freshly killed (by freezing) *M. domestica* pupae provided.

4.3.3. Miniplot Study

Eleven treatments (10 replicates per treatment) were established (Table 4.1) to test hypotheses relating to the biological control of non-native slugs and the impact of alternative prey on pest consumption by a generalist predator. The experiment was conducted under approximately 60% shade on black tarp overlaying rock at the Horticultural Research Farm in Fayette County, Kentucky (GPS: 37°58'N 84°32'W) (Figure 4.1).

Figure 4.1. Miniplot study to measure biological control capacity of *Scarites quadriceps* Chaudoir (Coleoptera: Carabidae) against *Deroceras reticulatum* Müller (Stylommatophora: Agriolimacidae) on *Hosta* 'Red October' with and without the presence of alternative prey in greenhouse at University of Kentucky Horticultural Research Farm.

The miniplots were circular plastic containers (26 cm diameter × 22 cm deep) with twelve drainage holes around the base and sides covered with organza fabric to prevent slugs from escaping from the containers. The inner rim of each miniplot container was painted weekly with FLUON (polytetrafluoroethylene; Whitford Corporation, Elverson, PA, USA) to prevent emigration of the slugs and carabid beetles from the experimental containers. A 10 cm^2 refuge (2.5 cm white foam board) was placed in the center of all miniplots and adjacent to the *Hosta* plant. The ground surrounding the experimental plots was liberally treated with Sluggo® slug and snail bait (Monterey Lawn and Garden Products, Inc., Fresno, CA, USA) to prevent slugs and snails from immigrating into the miniplots from the surrounding environment. Paint strainers (approximately 19 L) were placed around all miniplots (including controls) following the addition of slugs to prevent birds and other predators entering the miniplot containers. The trial was conducted in a complete randomized block design (Figure 4.2).

One *Hosta* ‘Red October’ was planted within each miniplot. The *Hosta* plants were obtained from Bloomin’ Designs Nursery (Auburn, GA, USA) when the plants were approximately eighteen months of age and immediately transplanted into Evergreen organic humus. When the *Hosta* was transplanted, the container was half-filled with humus. The plants were tied to wooden rods in order to prevent leaves from overhanging the containers and were allowed to stabilize in the miniplots for one week prior to experimentation. The slugs were introduced into the miniplots after one week. Treatments were divided into high (10 slugs) and low (5 slugs) slug densities. The female beetles were introduced 24 h after the slugs in order to allow colonization of the miniplot by slugs prior to the introduction of the epigean predators (carabids). All miniplots were watered every other day to ensure *Hosta* survival and to encourage the activity of the animals. Weeds were removed from all miniplots every other day to ensure food sources and refuges were consistent between miniplots.

The female carabids were starved for three days prior to addition to the plots and all beetles and slugs were weighed on a Mettler AE100 electronic analytical balance

(Mettler Instrument Corporation, Hightstown, NJ, USA) accurate to 0.1 mg prior to introduction into the miniplots. The mean slug biomass added to treatments with high slug densities was 93.94 mg ± S.E. 13.6. The mean slug biomass added to treatments with low slug densities was 74.77 ± S.E. 15.48. Despite randomization of slugs and chance allocation to treatments, there were significant differences between the mean biomass added to some treatments having both high (ANOVA, $F_{3, 394} = 3.68$, $P = 0.012$) and low (ANOVA, $F_{3, 197} = 5.75$, $P = 0.001$) slug densities. In treatments having low slug densities, the mean biomass of slugs introduced into Treatment 2 was significantly lower from that introduced into Treatments 4, 8, and 9. In treatments having high slug densities, the mean biomass of slugs introduced into Treatment 10 was significantly lower from that introduced into Treatments 3, 5, and 7.

Dipteran pupae were washed prior to addition and were added when beetles were introduced and were replaced every third day. After three weeks, miniplots were removed from the field. All the beetles and slugs remaining were collected through hand-sifting and weighed as described above. Leaves were removed from the plants and leaf area was measured by a LI-3100 electronic area meter (LI-Cor, Inc., Lincoln, NE, USA) accurate to 1.0 mm^2. A copy of each damaged leaf was made using a photocopy machine. The leaf copies represented the leaf prior to feeding damage. Leaf damage was recorded and measured by the percent loss to total leaf area.

Table 4.1. Invertebrates and their densities added to each of ten replicate miniplots pretreatment with one *Hosta* 'Red October' planted in each miniplot.

Treatment	Diet
1	No invertebrate species added
2	*D. reticulatum* (low density: 5) + *S. quadriceps* (1) + Dipteran pupae
3	*D. reticulatum* (high density: 10) + *S. quadriceps* (1) + Dipteran pupae
4	*D. reticulatum* (low density: 5)
5	*D. reticulatum* (high density: 10)
6	*S. quadriceps* (1)
7	*D. reticulatum* (high density: 10) + *S. quadriceps* (1)
8	*D. reticulatum* (low density: 5) + *S. quadriceps* (1)
9	*D. reticulatum* (low density: 5) + Dipteran pupae
10	*D. reticulatum* (high density: 10) + Dipteran pupae
11	*S. quadriceps* (1) + Dipteran pupae

Replication 1

4	9	3	11
8	5	1	10
6	7	2	

Replication 2

9	4	10	7
3	1	2	11
6	5	8	

Replication 3

2	4	10	9
1	7	8	6
11	3	5	

Replication 4

9	6	8	2
10	5	11	7
4	3	1	

Replication 5

6	8	4	1
9	10	3	2
11	5	7	

Replication 6

6	10	1	11
8	4	7	5
3	2	9	

Replication 7

6	3	9	7
2	1	11	5
4	10	8	

Replication 8

6	9	1	8
10	4	7	5
2	3	11	

Replication 9

1	6	5	11
3	10	2	8
9	7	4	

Replication 10

2	11	8	4
6	1	10	7
5	3	9	

Treatment Allocations

1 No invertebrates added
2 D. reticulam. (5) + *S. quadriceps* (1) + Dipteran pupae
3 D. reticulatum (10) + *S. quadriceps* (1) + Dipteran pupae
4 D. reticulatum (5)
5 D. reticulatum (10)
6 S. quadriceps (1)
7 D. reticulatum (10) + *S. quadriceps* (1)
8 D. reticulatum (5) + *S. quadriceps* (1)
9 D. reticulatum (5) + Dipteran pupae
10 D. reticulatum (10) + Dipteran pupae
11 S. quadriceps (1) + Dipteran pupae

Figure 4.2. Miniplots in greenhouse at the University of Kentucky Horticultural Research Farm in Fayette, County, Kentucky. Each replicate contained one of each of the eleven treatments.

4.3.4. Statistical Analysis

ANOVA was run on Minitab (Minitab Inc., State College, PA, USA) to compare slug biomass introduced into each treatment and test for effects of treatment on the percent leaf area loss per replication (with data arcsine transformed prior to analysis) and *D. reticulatum* eggs laid. Means were compared using post hoc Least Significant Difference for $P < 0.05$. A paired t-test for $P < 0.05$ was run on Minitab to compare mean total slug biomass before and after the experiment to test the efficacy of *S. quadriceps* as a predator of *D. reticulatum*.

4.4. Results

4.4.1. Leaf Area Loss

There were highly significant differences in percent leaf area damaged between treatments (ANOVA, $F_{10, 97} = 2.68$, $P = 0.006$). The three treatments without slugs sustained the least damage. One replicate (area loss = 50.6 mm^2) was excluded from Treatment 1 (*Hosta* control) as an outlier due to the presence of yellowstriped armyworm [*Spodoptera ornithogalli* Guenée (Lepidoptera: Noctuidae)] in the plot, causing damage which far exceeded the area loss sustained from feeding by *D. reticulatum* alone. The greatest leaf area damaged was observed in Treatments 4 (*D. reticulatum*: low density) and 5 (*D. reticulatum*: low density). There were no significant difference between these treatments and the other treatments containing slugs; however, these two treatments are significantly different from the control treatments (Figure 4.3).

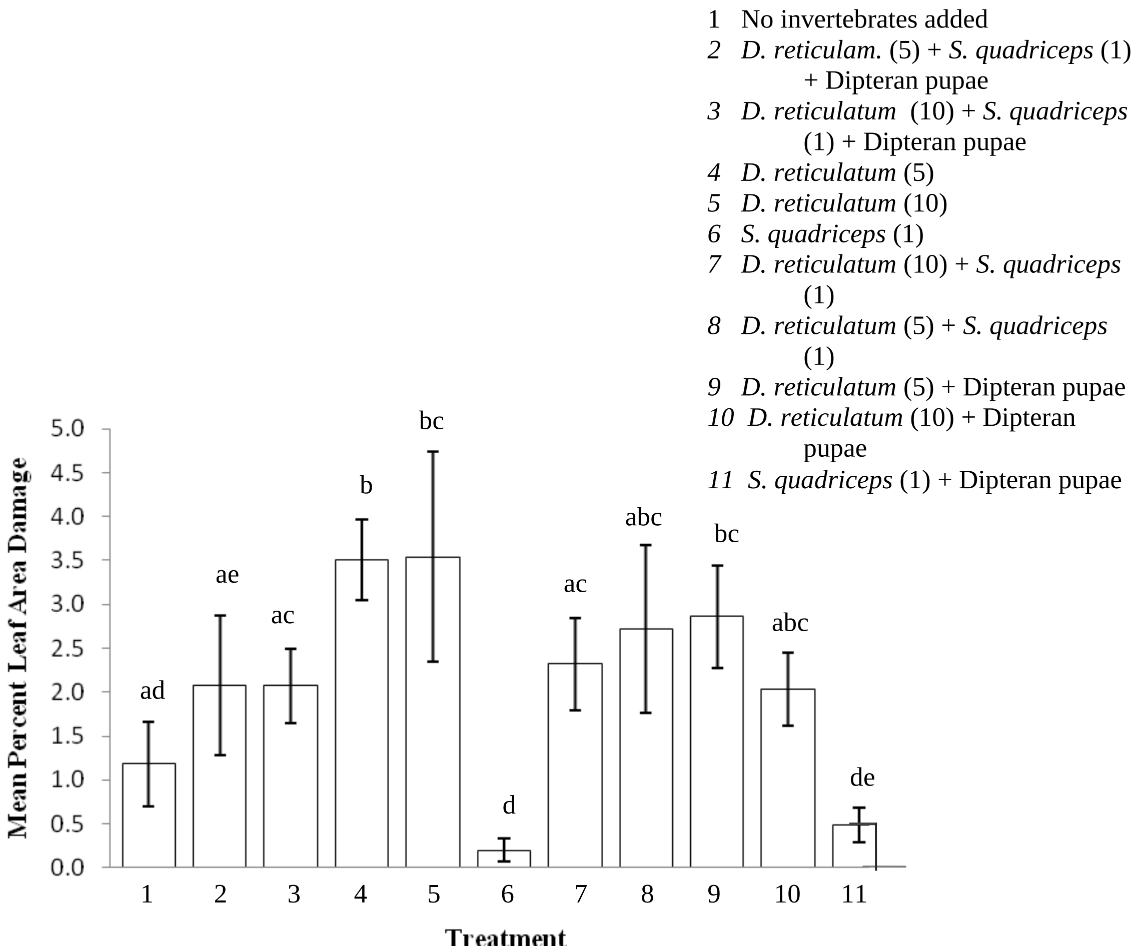

Figure 4.3. Mean percent leaf area damage (± SE) on *Hosta* ‘Red October’ by *Deroceras reticulatum* Müller (Stylommatophora: Agriolimacidae) by treatment with and without the predatory threat of *Scarites quadriceps* Chaudoir (Coleoptera: Carabidae). *Musca domestica* (Linnaeus) (Diptera: Muscidae) pupae provided as alternative food source for beetles. Letters above bars correspond to statistical differences between treatments.

Using LSD to compare the effect of slug population size on *Hosta* damage, I found no significant difference between treatments. There were significant differences (paired *t*-test $t_{14} = 6.17$, $P < 0.001$) between mean total slug biomass at the beginning of the study (48730.8 mg) to (1194.8 mg) at the end of the study.

4.4.2. Egg Production of *D. reticulatum*

At the conclusion of the study, any *D. reticulatum* eggs found were counted; however, the data was not normally distributed and insufficient to run statistical analyses of means.

4.4.3. Egg Production of *S. quadriceps*

S. quadriceps eggs and larvae were collected from the miniplots at the conclusion of this study; however, the data was not normally distributed and insuficient to run statistical analyses of means.

4.5. Discussion

In order to measure the biological control capacity of the generalist North American predator *S. quadriceps* against non-native slug populations of varying densities, herbivory on young *Hosta* plants by the non-native slug *D. reticulatum* and the effect of this native carabid on leaf area damage were compared. The hypotheses that the presence of carabid beetles will significantly reduce leaf herbivory by these molluskan pests was tested along with the hypothesis that diversifying this generalist beetles' diet with an alternate food source will lead to an increase in plant damage by disrupting the slug – carabid trophic pathway. This study found that the heaviest slug damage occurred in treatments with high and low slug densities, but without predators, supporting the hypothesis that the maximum amount of damage would be sustained in miniplots lacking the predatory threat of *S. quadriceps* (a known predator of slugs).

There was no significant difference in mean percent leaf area loss between treatments containing both slugs and beetles and the *Hosta*-only control, supporting the hypothesis that *S. quadriceps* is an effective biological control agent in suppressing *D. reticulatum* populations, thereby decreasing slug feeding on *Hosta*. This hypothesis is further supported by the significant difference between the mean total slug biomass prior to and at the conclusion of the study. As there is evidence to support even greater pest control in multi-predator ecosystems (Snyder *et al*. 2006), this may even be an underestimate of the control potential *S. quadriceps* would have in the field.

However, these results may be inconclusive as there was a significant difference between treatments containing beetles and slugs and those controls which contained beetles, but no slugs. This data suggests that while the controls were not significantly different from each other, Treatment 1 may have suffered a higher level of damage inflicted by yellowstriped armyworm larvae than the two other control treatments. Further research is needed which takes into account the previously unknown threat these Lepidopteran larvae pose to *Hosta* in order to explain the discrepancy.

As previously noted, the three treatments acting as controls (Treatments 1, 6, and 11), as well as *Hosta* in other treatments, sustained damage in the course of the study. This damage can be accounted for by the presence of yellowstriped armyworm larvae in the miniplots. The eggs of this species must have been laid in the miniplots in the interval of time between when the miniplots were placed in the greenhouse and when they were covered with paint strainers. Some damage to the *Hosta* plants was indistinguishable from slug damage; however, any damage to the outer edge of the leaf was most likely inflicted by armyworms and therefore not measured in this study. Despite the damage inflicted by the armyworms to these three treatments, the percent leaf area loss was still less than that inflicted in treatments containing *D. reticulatum*. Though the three control treatments most likely sustained damage from armyworms, the highest leaf area loss in these treatments occurred in Treatment 1. This disparity in the level of damage may be due to potential feeding by the generalist predator *S. quadriceps* on armyworm larvae or eggs, which further demonstrates the efficacy of this predator as a biological control agent.

In treatment comparisons where the only difference was slug density, there was no significant difference in mean percent leaf area loss, implying population size does not significantly influence slug damage to *Hosta*. This suggests that there was no significant correlation between slug population size, predation by carabid beetles, and plant damage.

However, damage to *Hosta* stalk and root system was not measured, therefore with higher densities, some slugs may have left the leaf area in favor of more isolated feeding locations.

There was also no significant difference in mean percent leaf area damaged between treatments containing alternative food sources for the carabid predator and those in which slugs were the only available prey. These results further support the use of native carabid species as conservation biological control agents despite their generalist feeding preferences. In fact, as this beetle is a generalist predator, alternative food sources may make *S. quadriceps* more effective as a biological control agent if this food is non-preferred to slug pests (Symondson *et al*. 2000) by providing the predators with food when slug densities are low.

Unfortunately, the duration of this study was too short to see the positive long term effects of an increase in carabid population density on slug population sizes. However, Symondson *et al*. (2000, 2002) found that carabid beetles using alternative prey to supplement their diet is beneficial to their survival. Had beetle egg production been higher, there might have been some increases in slug predation in the study as both adult and immature insects may impact the population size of a pest species (Harwood *et al*. 2007) and carabid larvae have been shown to feed on slugs and slug eggs.

The effectiveness of the nematode *P. hermaphrodita* as a successful biological control agent against pestiferous gastropod species in Europe should serve to stress the importance of finding such a species in this country (Rae *et al*. 2007). With the increase in introductions in North America by non-native gastropods, it is imperative that researchers find and test effective biological control agents, such as carabid beetles, as quickly as possible. In so doing, a way to better safeguard the commodities at risk from these non-native species (whose cash receipts in Kentucky and the rest of the country total millions of dollars in revenue) may be found. The role of carabid beetles as predators of slugs has been previously documented (Davies 1953, Mead 1961, Stephenson and Knutson 1966, Tod 1970, Cornic 1973, Tod 1973, Baronio 1974, Mead 1979, Symondson *et al.* 1996, 2000, McKemey *et al.* 2001, Paill *et al.* 2002, Symondson 2002a, 2002b, Oberholzer *et al.* 2003, Chabert and Beaufreton 2004, Chabert and Gandrey 2004, Choi *et al.* 2004, Dodd *et al.* 2004, Foltan *et al.* 2004, King *et al.* 2004). North American studies, such as this one, into the efficiency of these predators as conservation biological control agents is imperative if land managers are to take advantage of a predatory arthropod which is so plentiful in this country. By demonstrating an increase in mean *Hosta* leaf damage without the predatory threat of *S. quadriceps*, this study supports the theory that these beetles could be excellent candidates for native biological control agents against the non-native slug *D. reticulatum* in North America. However, much more research is needed into effective biological control agents to safeguard American commodities from this non-native pest species.

Chapter Five: Conclusions

The objectives of this study were to demonstrate the quantitative effects of dietary diversification on the survival, development, and fecundity of *D. reticulatum*. The hypothesis that a diverse diet is beneficial for this species and allows these generalist herbivores to fulfill their nutritional requirements more effectively than a single-source diet through dietary mixing was tested. However, in this study dietary diversification did not significantly correlate with development or fecundity. This may due to the addition of a nutrient-rich alternative food source in *Hosta* treatments to promote growth and reproductive development. It may also be a result of the close relationship between *Hosta* varieties.

Unlike previous studies which suggested *D. reticulatum* is a primarily outcrossing species, results in this study showed significantly higher egg production for individuals kept in self-fertilizing experimental conditions, as opposed to those kept in breeding pairs, which had the opportunity to outcross. This information could elevate the potential threat of *D. reticulatum* to agricultural and horticultural commodities as the liklihood that this species will self-fertilize means it is capable of more efficiently colonizing new areas. One of the limiting factors which determines whether a non-native species will be invasive is the ease with which it can establish a new population. *D. reticulatum* seems to have overcome that density-dependent limiting factor.

Another objective of this study was to quantify the biological control capacity of a native North American generalist predator, *S. quadriceps*, against non-native slug populations and the subsequent effect on plant growth and development. This experiment compared herbivory on *Hosta* 'Red October' leaves by the non-native slug *D.*

reticulatum and the effect of *S. quadriceps* on levels of plant damage, testing the hypothesis that the presence of these carabid beetles significantly reduces slug herbivory. While overall plant damage appeared minimal, even a small amount of slug herbivory lowers the aesthetic value of these ornamental plants, resulting in damage to a plant that may only produce 5 to 10 new leaves each growing season. In this study, results showed a significant difference in plant damage, with more damage occurring in treatments lacking the predatory threat of *S. quadriceps.* As there was no significant difference in plant damage between treatments containing an alternative prey choice for *S.* quadriceps, this study suggests that dietary diversification for this predator will not disrupt the slug – carabid trophic pathway. They may in fact be more efficient natural biological control agents if they are able to use alternative prey to sustain their populations when slug density is low. These predators are present in high numbers in Kentucky agricultural systems and techniques, such as mulching, that may increase their densities could result in inexpensive conservation biological control of non-native slug species. In conclusion, the complex life history and diet of terrestrial slugs allows researchers unique opportunities to study reproductive processes and tritrophic interactions in order to better understand the biology of pestiferous species and their predators.

Appendix A: A Field Guide to the Slugs of Kentucky

by

Rory J. Mc Donnell [1], Anna K. Thomas [2] and James D. Harwood [2]

[1] Department of Entomology, University of California, Riverside, California 92521, U.S.A.

[2] Department of Entomology, University of Kentucky, Lexington, KY 40546-0091, U.S.A.

Corresponding Author

James D. Harwood

Department of Entomology

University of Kentucky

Lexington, KY 40546-0091

E-mail: james.harwood@uky.edu

(1) Introduction

(a) Slug biology, ecology and pest status

Slugs are soft bodied gastropods (Mollusca) with rasping mouthparts, and two pairs of tentacles (Fig. 1). The animal's eyes are located on the uppermost, longer pair which are called ocular tentacles, while the lower pair, called peduncular tentacles, have a sensory function. A slug breathes through a small hole called a pneumostome that is located on its mantle, the flap of tissue behind the head (South, 1992). All species are capable of producing thick mucus that aids in moisture retention as well as movement, defense, and reproduction (South, 1992; Gordon, 1994). Slugs are hermaphroditic; when environmental conditions are adverse sexual reproduction (e.g. food is limiting or during periods of extreme climate such as high temperature or low rainfall), a slug can self-fertilize and produce viable offspring (South, 1992). Slugs prefer cool, dark and moist habitats and activity patterns tend to be highly variable throughout the day, but greatest immediately after sunset and during the hours proceeding dawn (South, 1992). When temperatures increase or conditions become too dry, they coat themselves with mucus to prevent desiccation and undergo aestivation. During this time they remain contracted and immobile. Typically, aestivation will occur in the soil; however, some slugs can aestivate while being attached to stationary objects such as rocks and stones.

Terrestrial slugs usually lay their eggs in holes or underneath debris and the number of eggs per batch and the number of batches vary between individuals (South, 1992). For example, according to Carrick (1938), *D. reticulatum* can lay up to 500 eggs per year and Davies (1977) states that *A. hortensis* lays from ten to thirty eggs per batch in captivity. Hatchling slugs appear very similar to adult slugs, with only size and slight differences in color pattern distinguishing them from their mature counterparts. The time necessary to reach sexual maturity and the natural life span of slugs varies between species as some slug species, such as *D. reticulatum*, have an annual life cycle, while others, such as *L. maximus*, have a biennial or plurennial life cycle.

Slugs occur throughout temperate and tropical regions, and are present in a range of habitats including forests, grasslands, river edges and areas characterized by high levels of anthropogenic disturbance (e.g. urban gardens, plant nurseries, garden centers and agroecosystems). Generally, invasive species are found in disturbed habitats such as urban and agricultural areas; native species dominate the malacofauna (DEFINE) in more remote locations such as old growth forests (Kappes, 2006).

Slugs are well known agricultural pests all over the world attacking a wide range of agricultural and horticultural crops (Barker, 2002; Godan, 1983 and South, 1992). For example, *D. reticulatum* can be responsible for up to one-third of winter wheat seed and seedling losses in the United Kingdom and other temperate climates (Port and Port, 1986; Glen, 1989; Brooks *et al*., 2005). In North America, evidence for the agronomic impact of slugs is less widely reported but invasive mollusks are responsible for significant losses to soybean (Hammond *et al.*, 1999), legumes (Byers *et al*., 1985), corn (Hammond & Stinner, 1987), alfalfa (Barratt *et al*., 1989), tobacco (Mistic & Morrison, 1979) and strawberries (Prystupa *et al.*, 1987; Duval & Banville, 1989). Such losses are likely to increase in significance as production systems diversify and agricultural practices increasingly adopt organic, low-input and/or minimum tillage approaches. In 1985, losses equivalent to $14 million to potato crops and $5 million to winter wheat were recorded in Great Britain alone (Port & Port, 1986) and slugs are also widely regarded as important pests of leeks, potatoes, onions, artichoke, brassicas, carrots, celery, cucumbers, chicory and runner, broad, and French beans, (reviewed by South, 1992). Moreover, slugs are also important pests in the horticultural and floricultural industries with primulas, campanulas, saxifrage and Michaelmas daisy often sustaining significant levels of aesthetic damage (Barnes and Weil, 1945). Although they sometimes consume mature foliage and flowers (Eaton and Tomsett, 1976; Anonymous, 1979), damage typically occurs during the seedling stage (Anonymous, 1979). On flowering plants and ornamentals, slugs will also often feed on bulbs, corms, and tubers.

In addition to direct yield losses resulting from feeding activities, slugs vector several plant diseases. Wester *et al.* (1964) reported that slugs are capable of transporting downy mildew to lima beans and Hering (1969) reported that *D. reticulatum* and *A. hortensis* spread the fungus *Botrytis* along grapevines. They also transmit brassica dark leaf spot (Hasan and Vago, 1966), carrot licorice rot (Dawkins *et al*., 1985) and bacterial soft rot (Dawkins *et al.*, 1986). Slugs can pose potential health risks to humans by vectoring certain pathogens. Sproston *et al.* (2005) demonstrated the ability of *D. reticulatum* to vector *Escherichia coli* 0157. The slugs came into contact with the pathogen on sheep feces and then transferred it to vegetables where the bacteria remained viable for several days. This ability to vector disease and bacteria further highlights the potential adverse impacts of invasive slugs in the U.S. Finally, important commodities grown throughout Kentucky have been reported as food resources for many invasive species known to occur within the state; therefore, economic losses are likely to increase in future years because of changing agricultural production practices and more favorable climatic conditions.

(b) Slug collecting

A range of sampling techniques can be utilized to collect slugs. Although the vast majority of species are nocturnal, specimens can easily be found during the day by searching under sources of cover in suitable habitats *e.g.* flower pots in garden centers, decaying wood in forests and in sprinkler valve boxes in urban gardens. A number of authors (South, 1964; Hunter, 1968; Rollo and Ellis, 1974) have successfully used soil cores to sample slug communities. This method involves removing a turf-soil core (e.g. 10 cm x 50 cm) and gently washing it in a fine-meshed sieve with water. This technique is an important tool for collecting species such as *T. budapestensis* and *Testacella haliotidea* Draparnaud which are predominantly subterranean. Baited traps, consisting of cat/dog food or organic vegetables covered with black plastic sheeting, can also be used to collect specimens (Mc Donnell *et al.*, 2008). The food provides an attractant for slugs while the plastic sheeting provides suitable shelter and maintains a high humidity. Since certain behavioral characteristics (*e.g.* response to a continuous disturbance) are important in identifying some species, specimens should be kept alive in containers (*e.g.* 15 cm x 15 cm x 15 cm) lined with damp paper towel and fed on organic vegetables, oatmeal and/or pet food. For additional information on establishing and maintaining slug colonies, see Sivik (1954) and Stephenson (1962).

(c) Slug preservation and dissection

Some slug species such as *A. hortensis* are difficult to identify solely on external morphological traits; dissection and examination of genitalia is necessary in some cases to make positive identifications. However, before specimens are preserved, detailed notes should first be made on collection locale, date, slug size and the color of both the general body and mucus, as such information can prove to be very useful at a later date (colors tend to fade over time with storage in alcohol). It is also a good idea to take a photograph of the dorsal, ventral and right side of the slug.

Specimens for preservation should be placed into a jar that has been filled to the brim with boiled water that has been allowed to cool. Seal the jar for approximately 24 h, then remove the slug and place it in 70% ethanol. This ensures that the slugs will be extended and easier to dissect than if placed directly into alcohol. If specimens are required for molecular studies, the tip of the tail should be excised prior to preservation and placed in 100% ethanol (Mc Donnell *et al.*, 2009). The remainder of the slug should be preserved as above.

To prepare a Petri dish for the dissection, hot wax can be poured to a depth of ~5 mm and allowed to solidify. The slug is then placed onto the wax surface, its body straightened and pins inserted through the head close to the tentacles and close to the tip of the tail. Water is added until it covers the specimen. A fine scalpel is used to make an incision just above the genital pore (Fig. 1), the dissection then continues beneath the entire mantle and then upwards to a point just posterior to the end of the mantle. This flap of tissue can now be peeled back to view the internal organs. The genitalia are white (Fig. 2) and can be traced back from the genital pore. For additional details on slug dissecting techniques, see Kerney and Cameron (1979).

(d) External and internal anatomy

The external morphology of a typical slug is illustrated in Figure 1. Figure 2 shows the genital structure of *L. maximus*. The ligula or stimulator, which is important in identifying certain arionids and milacids can be viewed by cutting open the atrium. The atrium also contains the epiphallus structure (at the outlet of the epiphallus) which is important in identifying the different species of the *Arion hortensis* complex (see below for details). In addition, a finger-like projection called the flagellum is present on the penis of certain species recorded in Kentucky *e.g. Lehmannia valentiana* (d'Audebard de Férussac). Additional detail on the internal anatomy of the various slug families and species can be found in Backeljau and Van Beeck (1986), Barker (1999), Kerney and Cameron (1979), Pinceel *et al.* (2004) and Quick (1960).

(e) Status of slugs in North America

Slugs in the subfamily Ariolimacinae (*Ariolimax*) and the genera *Prophysaon*, *Anadenulus*, *Binneya*, *Hemphillia*, *Hesperarion*, *Philomycus*, and *Pallifera* are all native to North America (South, 1992; Mc Donnell *et al*., 2009). In contrast, the invasive U.S. fauna consists primarily of European species such as *Arion distinctus* Mabille, *Arion fasciatus* (Nilsson), *Arion hortensis* (Ferussac), *Arion intermedius* (Normand), *Arion rufus* (Linnaeus), *Arion subfuscus* (Müller), *Deroceras panormitanum* (Lessona and Pollonera), *Deroceras reticulatum* (Müller), *Limax maximus* (Linnaeus), *Milax gagates* (Draparnaud), *Tandonia budapestensis* (Hazay) (Reise *et al.*, 2006; Mc Donnell *et al*., 2009) and tropical species such as *Veronicella cubensis* (Pfeiffer) (Mc Donnell *et al.*, 2008). Robinson and Slapcinsky (2005) estimated that there are currently over 80 established species of exotic slugs and snails established in the US and Canada (excluding the Hawaiian Islands and Puerto Rico). These invasive species include the slug, *Deroceras laeve*, which is considered both native and exotic to North America as some populations have been introduced very recently and have subsequently expanded their range (South, 1992).

The following species of invasive slugs are **known** to occur in Kentucky (Burch 1962; Branson & Batch 1969; Mc Donnell *et al*. 2008; Thomas & Harwood, unpublished data) although others are likely present but have not been reported in the literature (see Key to Genera and Species, which includes a description of those species likely to occur):

Arion hortensis

Arion intermedius

Arion subfuscus

Deroceras laeve

Deroceras reticulatum

Lehmannia valentiana

Limax flavus

Limax maximus

Milax gagates

For information on the native slug fauna of the state see Section 3 below.

Due to increased global trade, international trade agreements and tourism, invasions by non-native gastropod species continue to be a persistent problem throughout the United States. Robinson (1999) listed 4,900 gastropods intercepted at points of entry into the United States from 100 countries between 1993. Gastropods can also be accidentally transported with plants. For example, one cardboard box of ash saplings shipped from California to Massachusetts in September 2005 was found to contain five species of snails, three species of slugs and several eggs (Gary Bernon, USDA-APHIS, pers. comm.). Such interstate transportation of slugs highlights the urgent need for more effective monitoring of shipments at state and national borders.

(2) Identification Key to Family, Genus and Species

This guidebook provides a field identification key to the different families, genera and species of invasive slugs in Kentucky. Based on our collecting and research experience throughout the state and other parts of the U.S., it is the invasive fauna which is most damaging in terms of agricultural and horticultural production, with native species seldom reaching pest status. However, we also provide an identification key to native genera (*Philomycus* and *Pallifera*) and include a brief description of this fauna.

The families and species denoted by an asterisk in the key below are those which have not yet been recorded in Kentucky but are likely to be collected in the future. For all species, we provide diagnostic field characters and for problematic species (noted in the key) dissection is recommended to confirm identification.

(A) Key to Families

1. Slug with an external shell (Figure 3)……………..……………**Family Testacellidae***
   Slug without an external shell …………………………………………………………**2**

2. Slug with mantle covering most of the body………..…………..**Family Philomycidae**
   Slug with mantle covering no more than half of the body………..……………………**3**

3. Pneumostome located anterior to the mid-point of the mantle (Figure 4)
…………………………………...…………………………………… **Family Arionidae**
   Pneumostome located posterior to the mid-point of the mantle (Figure 5)…………… **4**

4. Mantle with a horse-shoe shaped furrow; keel runs from end of mantle to tip of tail
………... ………………………………………………………………… **Family Milacidae**
   Mantle without a horse-shoe shaped groove; keel shorter than above …..................... **5**

5. Mantle ridges/wrinkles centered to the right of the mantle over the pneumostome
……………………………………………………………………... **Family Agriolimacidae**
   Nucleus of mantle ridges lies on the mid-dorsal line ……………..…**Family Limacidae**

(B) Key to Genera and Species

(1) Family Agriolimacidae

1. Gray to cream in color (Figure 5), usually with dark reticulations; a white, very sticky mucus secreted when continuously disturbed; up to 5 cm in length ……………………………………………..……………… *Deroceras reticulatum*

Dark to light brown; mucus watery and colorless …………………….………. **2**

2. Tip of the tail rises vertically or may curve backwards away from the sole; rim of pneumostome may be paler than rest of body; sole grayish; body appears to be thin-walled giving a translucent appearance; up to 3 cm in length (Figure 6); **dissection required** ……………………………………………...….. *Deroceras panormitanum**

Tip of the tail slopes forward; rim of pneumostome usually the same color as the rest of body; sole light brown; body not appearing translucent; up to 2.5 cm in length (Figure 7); **dissection required** ……………………………..………………. *Deroceras laeve*

(2) Family Arionidae

1. Very large slug (up to 18 cm); often exhibits a 'rocking' motion when disturbed; orange to red, contrasting with duller body; foot fringe with thin, dark vertical lines (Figure 8); head and tentacles distinctly darker than rest of body; sole color usually matching upper surface; sole mucus very pale or colorless ……………………………………………………………..…..…...…. *Arion rufus**

Smaller slug; does not 'rock' when disturbed ……………………………………... **2**

2. Very small slug (≤ 2.5 cm) with an echinate, or spiny, appearance when contracted (use a hand lens); head and tentacles noticeably darker than rest of the body (Figure 9) ……………………………………………………………..……… *Arion intermedius*

Larger slug; not echinate when contracted ………………………...…...…..……... **3**

3. Dark, grayish brown to bluish black (Figures 10 & 11); mucus on sole bright yellow to orange ……………………………..…………………………………………………….... **4**

Lighter, grayish to yellowish brown (Figures 4 and 12); foot sole pale yellow or grayish white with colorless mucus …...………………………………..…………..… **5**

4. Tentacles bluish-black; body gray to brown in color (Figure 10) but with varying amounts of yellow granules which may cause a slightly yellowish coloration; back color *not* contrasting with lower sides; right mantle band *always* with a break above the pneumostome; up to 4cm in length; **dissection required** ……………………………..……………….. ……………..……….*Arion distinctus**

Tentacles faintly reddish; body gray to black in color (Figure 11); sides below the lateral bands contrasting pale; *never* a break in right mantle band above pneumostome; up to 5 cm in length; **dissection required** ………………………………… *Arion hortensis*

5. Slug contracts into a hemispherical shape when disturbed and is bell shaped in transverse section when at rest; body mucus colorless; sole grayish white; up to 5 cm in length (Figure 12) …………………..……………..……………………. *Arion fasciatus**

Slug unable to contract into a hemispherical shape when disturbed and is not bell shaped in transverse section when at rest; body mucus orange-yellow; foot sole pale yellow and sometimes translucent in appearance (Figure 4); up to 7 cm in length ……………………………………………………………..……..……. *Arion subfuscus*

(3) Family Limacidae

1. Body yellowish with distinct green mottling (Figure 13); tentacles contrasting oily blue; mucus slippery and plentiful; keel often marked by a pale yellow line (sometimes only obvious near the tip of the tail); mucus yellow; up to 12 cm in length ………………………………………………………………………..…… *Limacus flavus*

Body without green mottling; tentacles light to dark brown; mucus colorless ..……….**2**

2. Mantle spotted or marbled black; mucus sticky and sparse; keel obvious; lateral bands may be present on the tail but are always absent from the mantle (Figure 14); up to 20 cm in length …………………………....………………………..………..…… *Limax maximus*

Mantle with two obvious lateral bands present and a less distinct median band; mucus watery; keel poorly marked; lateral bands often run full length of the body (Figure 15); up to 7.5 cm in length ……………………...……………………...… *Lehmannia valentiana*

(4) Family Milacidae

Only *M. gagates* (Figure 16) has been recorded in Kentucky. See below for a full description of this and related species.

(5) Family Philomycidae

Key to Genera

1. Mantle covering the entire length of the body including the head; less than 4 cm in length ………………………………………..……………………….. Genus *Pallifera*

Mantle covering the body but not the head; greater than 4 cm in length ……………………………………………………………………......Genus *Philomycus*

(6) Family Testacellidae

Testcallid slugs have not yet been recorded from Kentucky but *Testacella haliotidea* Draparnaud (Figure 17) has been reported from other parts of the U.S. such as California (Mc Donnell *et al.*, 2009).

(3) Species Descriptions

Native Species

The native slug fauna of Kentucky has received relatively little research attention and the total number of native species present in the state remains uncertain due to the lack of systematic surveys and unstable taxonomy. However, *Megapallifera mutabilis* (Hubricht), *Megapallifera ragsdalei* (Webb), *Megapallifera wetherbyi* Binney, *Philomycus carolinianus* (Bosc), *Philomycus flexuolaris* Rafinesque, *Philomycus togatus* (Gould), *Philomycus venustus* Hubricht, *Philomycus virginicus* Hubricht, *Pallifera dorsalis* (A. Binney), *Pallifera fosteri* Baker, *Pallifera marmorea* Pilsbry and *Pallifera secreta* (Cockerell) have been reported from throughout the state (Burch, 1962; Hubricht, 1968; Branson and Batch, 1970; Branson, 1973; Branson and Batch, 1988; Dourson and Feeman, 2006). Detailed ecological information on these slugs is also scarce. *Philomycus carolinianus* and *P. flexuolaris* are thought to have a preference for moist upland wooded situations (Branson and Batch, 1988). The former species is commonly collected under the bark of hardwood logs on the floodplains of forests while the latter tends to shelter under rocks (Branson and Batch, 1970). Branson and Batch (1988) cited leaf litter in moist forests as a preferred microhabitat of *P. dorsalis* while *M. ragsdalei* was found most often in moist, wooded ravines and streamside buffs. All of these native species most likely feed on fungi and lichens in their woodland habitats (Runham and Hunter, 1970).

Invasive Species

The color of specimens described in the following biographies represents typical color forms of each of the species. Any variation from this in Kentucky specimens will be highlighted.

A. Family Agriolimacidae

(1) *Deroceras laeve* (Müller, 1774) - Figure 7

Global distribution: *Deroceras laeve* is native to the Holarctic (South, 1992) but has been introduced to most areas of the world (Barker, 1999).

Ecology: This partially amphibious species (Chichester and Getz, 1969) is found in an enormous range of habitats including marshes, wet woodlands, fields, and river banks (Cameron *et al.*, 1986; South, 1992) from sea level to altitudes of greater than 3 miles (Barker, 1999). It is a pest of agricultural and horticulture habitats, feeding on both living and dead plant material (Alicata, 1950). In its native range, *D. laeve* takes refuge under leaf litter and woody debris (Perez *et al*., 2008).

Description: *Deroceras laeve* can reach a length of 2.5 cm and has colorless mucus. Mantle covers approximately half the length of the body (Barker, 1999). Coloration is dark brown (Fig. 7) with distinctive black flecking but specimens can be gray, light brown or black. Sole tends to be light brown. The penis of *D. laeve* tends to be variable but it is usually long and slender with a simple appendage. However, some individuals may be solely female with vestigial male reproductive organs (Kerney and Cameron, 1979).

Similar Species: In other parts of the U.S., *Deroceras laeve* can easily be confused with *Deroceras panormitanum* (Lessona and Pollonera) but the latter has not yet been recorded in Kentucky. The structure of the penis is the most reliable way of distinguishing both species. A pneumostome with a distinctly paler rim has often been cited (e.g. Barker, 1999) as a reliable character for distinguishing *D. laeve* (absent) from *D. panormitanum* (present) but Mc Donnell *et al.* (2009) have found specimens of *D. panormitanum* in California lacking this trait and specimens of *D. laeve* with a pale rim. As a result, this character should be used with caution when identifying these species. De Winter (1988) cited the shape of the tip of the tail as a considerably more reliable character. In *D. panormitanum* it rises vertically from the foot and may curve backwards while in *D. laeve* the tail tip slopes forward.

(2) *Deroceras panormitanum* (Lessona and Pollonera, 1882) - Figure 6

Remarks: Not yet recorded in Kentucky.

Global distribution: This slug is native to southwestern Europe (Kerney and Cameron, 1979) but has been introduced to Canada, U.S.A, South America, New Zealand, Australia, South Africa and throughout Europe (Chevalier, 1973; Altena & Smith, 1975; Rollo & Wellington, 1975; Barker, 1999 and Forsyth, 2004).

Ecology: *Deroceras panormitanum* is found mainly in gardens, greenhouses, parks, and wastelands. It is also present in fields and hedges. The species is a serious pest of agriculture, horticulture and urban gardens (Barker, 1999).

Description: Up to 3 cm in length with colorless mucus (Barker, 1999). Body tends to be brown but can be gray (Fig. 6). Mantle is approximately ⅓ length of the body which appears to be thin-walled giving a translucent appearance (Forsyth, 2004). Sole light gray. Tip of the tail rises up vertically from the sole or may curve backwards away from it (de Winter, 1988). The penis of this species is bilobed and has 4-6 flagella between the lobes (Forsyth, 2004; Kerney and Cameron, 1979).

Similar Species: See *D. laeve* above.

(3) *Deroceras reticulatum* (Müller, 1774) – Figure 5

Global distribution: This species is native to the western Palaearctic region but is now present in most parts of the world (Quick, 1960; Barker, 1999 and Forsyth, 2004).

Ecology: This species is most abundant in synanthropic situations and is a common agricultural and garden pest. It feeds on most vegetable and grain crops as well as horticultural plants (South, 1992; Gordon, 1994). While most slugs present in gardens feed at ground level or just below its surface, *D. reticulatum* will crawl up plants to feed (Barnes and Weil, 1945).

Description: Up to 5 cm in length (Barker, 1999). Mucus is clear but becomes milky with continuous disturbance. Body color ranges from cream (Fig. 5) to gray but specimens usually with dark reticulations. The penis is relatively large and has a bilobed appearance (due to a constriction at its midpoint). There is usually a single flagellum which may have a number of bulbous branches (Forsyth, 2004; Barker, 1999).

Similar Species: This species with its milky colored mucus is unlikely to be confused with any other slug in Kentucky.

B. Family Arionidae

(1) *Arion distinctus* Mabille, 1868 – Figure 10

Remarks:

(a) Not yet recorded in Kentucky

(b) This species is part of a species complex (Davies, 1977 and 1979) containing *A. hortensis s.s., A. distinctus* and *Arion owenii* Davies. Prior to taxonomic separation by Davies (1977, 1979), the three species were grouped together under *Arion hortensis s. l.* As such pre-1977 records of *A. hortensis* should be treated with caution.

Global distribution: This species is native to western Europe (Roth and Sadeghian, 2006) but has been documented in the U.S. (Roth, 1986; Mc Donnell *et al.*, 2009), Canada (Forsyth, 2004), New Zealand (Barker, 1999) and most of Europe including Belgium (Backeljau & Marquet, 1985; De Wilde 1983, 1986), Sweden (Davies, 1979), Norway (Holyoak & Seddon, 1983), and the Faroe Islands (South, 1992).

Ecology: This species is mainly found in areas associated with man (South, 1992) and is a serious pest of vegetable crops (Barker, 1999).

Description: Up to 4 cm in length. Mucus yellow to orange and very sticky (Barker, 1999). Body color is variable and ranges from dark gray to grayish brown (Fig. 10). Tentacles bluish-black. Back color *not* contrasting with lower sides. Right mantle band always with a break above the pneumostome.

Similar Species: In other parts of the U.S. this species can easily be confused with *A. hortensis* but the structure of the genitals can be used to reliably separate both species. Backeljau and Van Beeck (1986) cite the shape of the epiphallus structure (i.e. a structure associated with the outlet of the epiphallus in the atrium) as the most reliable diagnostic character. In *A. distinctus*, it is a relatively well-defined conical structure which extends into the atrium and covers the outlet of the epiphallus. In addition, a gutter runs from the margin of the epiphallus structure to its centre (Backeljau and Van Beeck, 1986). In the case of *A. hortensis*, the epiphallus structure covers about half of the outlet and the gutter is absent. The final member of the complex, *A. owenii*, has not yet been recorded in the U.S.A. It has a variable epiphallus structure but according to Backeljau and Van Beeck (1986) it is usually long, thin, tongue-like and protrudes from the outlet of the epiphallus.

(2) *Arion fasciatus* (Nilsson, 1823) – Figure 12

Remarks: Not yet recorded in Kentucky.

Global distribution: This species is widely distributed in Europe (Falkner *et al.*, 2001) and has been introduced into North America (Chichester & Getz, 1973).

Ecology: This slug is often associated with gardens, waste ground (Kerney & Cameron, 1979) and parks (Pfleger, 1999).

Description: Up to 5 cm in length. Grayish above but fading to paler gray on sides. Lateral bands dark but with a distinct yellow coloration below (Fig. 12). Right lateral band passes over the pneumostome. Sole whitish gray with colorless mucus. Bell shaped in transverse section when at rest.

Similar Species: There are two additional European invasive species, *Arion silvaticus* Lohmander and *Arion cirumscriptus* Johnston, which are externally similar to *A. fasciatus* and both have been recorded in the U.S (Roth and Sadeghian, 2006; Jass, 2007). However, the yellowish flush below the dark lateral bands is a useful trait for identifying *A. fasciatus* in the field. In terms of the genital morphology, the unpigmented epiphallus of *A. fasciatus* distinguishes it from the speckled epiphallus of *A. circumscriptus*. *Arion silvaticus* is also similar to *A. fasciatus* but it has a wider oviduct than the latter (Kerney and Cameron, 1979). It is worth highlighting that Geenen *et al.* (2006) have cast doubt on the species status of *A. circumscriptus*, *A. fasciatus* and *A. silvaticus*.

(3) *Arion hortensis* d'Audebard de Férussac, 1819 – Figure 11

Remarks:

(a) Recently reported from Kentucky (Mc Donnell *et al.*, 2008)

(b) A member of the *Arion hortensis* species complex (see *A. distinctus* above for details).

Global distribution: This species has been introduced into the U.S. (Roth, 1986; Thomas & Harwood, unpublished data), Canada (Forsyth, 2004), New Zealand (1999) and throughout Europe including Belgium (Backeljau & Marquet, 1985; De Wilde 1983, 1986), Ireland (Anderson, 2005), United Kingdom, Wales, France, and the Netherlands (Davies, 1979). It is native to western and southern Europe (Roth and Sadeghian, 2006).

Ecology: This species is common in areas associated with man and is a well-known agricultural and horticultural pest (Davies, 1979; Kerney & Cameron, 1979; South, 1992 and Barker, 1999).

Description: Up to 5 cm in length. Mucus yellow to bright orange and very sticky (Barker, 1999). The predominant body color of this species is black (Fig. 11) but it can also be various shades of gray. The color of the sides below the lateral bands are contrasting pale and there is never a notch in the right mantle band above the pneumostome. Tentacles faintly reddish. Internally, the epiphallus structure is an inconspicuous plate which covers about half of the epiphallus outlet and it never has a gutter (Backeljau and Van Beeck, 1986).

Similar Species: Easily confused with *A. distinctus* (see above).

(4) *Arion intermedius* Normand, 1852 – Figure 9

Remarks: Recently reported from Kentucky (Mc Donnell *et al.*, 2008)

Global distribution: This species has been documented throughout its native range of central and western Europe (Anderson, 2005; Backeljau, 1985; Barker, 1999; Kerney and Cameron, 1979; Solhøy, 1981). It has been introduced into Vancouver (Rollo & Wellington, 1975) and other areas in North America (Chichester & Getz, 1973, Mc Donnell *et al*., 2009; Thomas & Harwood, unpublished data) as well as Australia, New Zealand, South Africa (Barker, 1999), North Africa and Polynesia (Forsyth, 2004)

Ecology: This slug is common in woodland and grassland habitats. It also occurs in gardens and agricultural land, but it is less common in these areas (South, 1992). Barker (1999) suggests that *Arion intermedius* is not a significant pest.

Description: Up to 2.5 cm in length. The predominant color of the body and sole is grayish-yellow but the head has distinctly darker tentacles (Fig. 9). Body mucus yellow (Forsyth, 2004). *Arion intermedius* can be easily separated from other slug species by the presence of small spikes on the tubercles which give the slug an echinate appearance when it is contracted (Kerney and Cameron, 1979). Internally, there is no ligula within the genital atrium (Quick, 1960).

Similar Species: This arionid, with its echinate appearance, is unlikely to be confused with any other slug in Kentucky.

(5) *Arion rufus* (Linnaeus, 1758) – Figure 8

Remarks: Not yet reported from Kentucky

Global distribution: This species can be found throughout Europe, particularly in the south and has been introduced to the U.S. (Roth and Sadeghian, 2006) and Canada (Forsyth, 2004). It is native to western and southern Europe (Roth and Sadeghian, 2006).

Ecology: A species known from anthropogenic areas including campsites, gardens and parks (Forsyth, 2004). Mc Donnell *et al.* (2009) collected this species in coastal forests in northern California. It is omnivorous, feeding on fungi, faeces, carrion and both dead and living plants (Pfleger, 1999 and Forsyth, 2004).

Description: Up to 18 cm in length. Body color brownish to reddish orange. The distinct foot fringe is usually orange or red (contrasting with duller body) and has obvious black vertical lines (Fig. 8). Head and tentacles darker than the rest of the body. Body mucus is pale orange and sole mucus colorless. Specimens sometimes display a rocking behavior when disturbed.

Similar Species: *Arion rufus* is unlikely to be confused with any other slug species currently known from Kentucky but in Europe it is very similar externally to *A. lusitanicus* (= *vulgaris* Moquin-Tandon). Although not yet reported from the U.S., this species is a very severe pest in Europe and could be a likely future invasive species in Kentucky. Both species, however, can be reliably separated on the basis of genital morphology. *Arion rufus* has a large, relatively unsymmetrical atrium with a large ligula situated inside the genital atrium. The ligula of *A. lusitanicus* on the other hand is located inside the distal part of the oviduct giving it a swollen appearance. The point of insertion of the spermathecal duct and the epiphallus is lower on the atrium in *A. lusitanicus* than in *A. rufus* (Noble, 1992).

(6) *Arion subfuscus* (Draparnaud, 1805) – Figure 4

Remarks: This cryptic species is part of a complex containing two distinct species, *Arion subfuscus* and *Arion fuscus* (Müller) (Pinceel *et al*., 2004). Only *A. subfuscus* has been recorded in the U.S. (Pinceel *et al.*, 2005; Mc Donnell *et al.*, 2009).

Global distribution: This species is native to northern and western Europe (Roth and Sadeghian, 2006) and has been documented throughout Ireland (Anderson, 2005), Britain (Quick, 1960), Finland (Fosshagen et al., 1972), Spain, Portugal (Alonso, 1975; Seixas, 1976), the Balkan states (Osanova, 1970), and the former USSR (Likharev & Rammel'meier, 1952). It has been introduced into Canada (Rollo & Wellington, 1975, Forsyth, 2004) and other parts of North America (Roth and Sadeghian, 2006), New Zealand, and Venezuela (Chichester & Getz, 1973; Blanchard & Getz, 1979).

Ecology: This slug is found in many habitats, particularly forests and residential areas; however, it is scarce in agricultural fields (South, 1992; Thomas & Harwood, unpublished data). Mc Donnell *et al.* (2009) also collected this species in garden centers in northern California.

Description: Up to 7 cm in length. The body tends to be orange-brown (Fig. 4) often with darker lateral bands. Body mucus is orange-yellow and very sticky. Sole light yellow with colorless mucus. Foot fringe with thin lineolations. A good diagnostic feature for this species is its inability to contract into a hemispherical shape when disturbed or at rest (Cameron *et al.*, 1979). All other species of arionids known from Kentucky can contract into this shape when alarmed or resting.

Similar Species: *Arion subfuscus* can be distinguished from *A. fuscus* using the position of the genitalia relative to the digestive gland. For *A. subfuscus*, the genitalia are large, pale and are located on the edge of the digestive gland while those of *A. fuscus* are smaller, darker and embedded within the gland (Pinceel *et al.*, 2004).

C. Family Limacidae

(1) *Lehmannia valentiana* (d'Audebard de Férssac, 1823) – Figure 15

Global distribution: This slug is native to the Iberian Peninsula (Roth and Sadeghian, 2006) but has been introduced throughout Europe including Ireland (Anderson, 2005), Great Britain (Kerney, 1987), the Netherlands (Gittenberger & de Winter, 1980), Sweden (Waldén, 1960) and the Azores (Barker, 1999). Outside of Europe it has been recorded in the U.S. (Howe & Findlay, 1972; Chichester & Getz, 1973), Canada (Forsyth, 2004), Australia, New Zealand, South Africa, Columbia, Chile, Peru, Juan Fernandez and Easter Island (Barker, 1999).

Ecology: This slug is common in greenhouses and is frequently found in residential gardens (reviewed in detail by South, 1992).

Description: Up to 7.5 cm in length. The ground color is usually buff but can also be brown. This species generally has two distinct, parallel lines on its dorsal surface which often run the full length of the body (Fig. 15). There may also be a less obvious median band. The mucus of *L. valentiana* is profuse, colorless and watery. Internally, the penis has a short, blunt flagellum (Forsyth, 2004).

Similar Species: In Kentucky, this species could be confused with *Limax maximus* L. but the latter is larger, never has mantle bands and has sticky mucus (see below for extra detail). *Lehmannia nyctelia* (Bourguignat) is native to Europe and may eventually be introduced to the U.S. Externally, it is almost identical to *L. valentiana* but the penis of *L. nyctelia* does not have a flagellum. However, Mc Donnell *et al.* (2009) have collected specimens of this species in California where the flagellum has been inverted into the lumen of the penis giving the appearance of *L. nyctelia.* In cases where no flagellum is visible, collectors are welcome to send specimens to the senior author for confirmation.

(2) *Limacus flavus* (Linnaeus, 1758) – Figure 13

<u>Global distribution:</u> *Limacus flavus* is native to Europe (Roth and Sadeghian, 2006) and has been documented in Great Britain (Kerney, 1976), the Crimea, the Caucasus, the Near East, North Africa (Likharev & Rammel'meier, 1952), Denmark, and Scandinavia (Kerney & Cameron, 1979). It has been introduced into Australia (Altena & Smith, 1975), New Zealand (Barker, 1982), North and South America (Chichester & Getz, 1973), South Africa (Quick, 1960), St. Helena (Gittenberger, 1980), China, Japan (Forsyth, 2004), Madagascar, Rarotonga and Vanuatu (Barker, 1999).

<u>Ecology:</u> This highly invasive species is strongly associated with synanthropic areas. It is a pest of stored agricultural produce (Godan, 1983) and both residential and commercial areas (Barker, 1999). In Europe, it is known from woodlands (Quick, 1960) and in Armenia, it was found in subalpine and steppe zones in cracks in cliffs (Likharev & Rammel'meier, 1952).

<u>Description</u>: Up to 12 cm in length and mottled yellow and green (Fig. 13). Body mucus yellow but sole mucus colorless. Tentacles contrasting blue. Keel weak, rounded and often marked by a yellow line. Internally, the penis is long with 2-3 kinks and the spermathecal duct joins at the apex of the oviduct (Kerney and Cameron, 1979).

<u>Similar Species</u>: This species with its yellowish-green mottling is very unlikely to be confused with any other slug species in Kentucky.

(3) *Limax maximus* Linnaeus, 1758 – Figure 14

<u>Global distribution:</u> *Limax maximus* has been documented throughout Europe [reviewed in detail by South, 1992] and has been introduced into North and South America (Chichester & Getz, 1973), South Africa (Quick, 1960), Australia (Altena & Smith, 1975), New Zealand and Canada (Barker, 1999).

<u>Ecology:</u> A synanthropic species which occurs in parks, gardens, greenhouses, outhouses, cellars, greenhouses, underground tunnels and woodlands close to residential areas (Quick, 1960; South, 1992; Pfleger, 1999 and Barker, 1999). It may be a pest of agriculture and horticulture (Barker and McGhie, 1984). *L. maximus* has a unique mating

ritual. Unlike most slugs, which mate on the ground or under the earth, this species mates while suspended on a thick mucus strand in the air, often under an overhanging branch or post (Runham & Hunter, 1970).

Description: Up to 20 cm in length. Body color pale brown with distinctly darker bands on the tail which may be fragmented into spots. Mantle never with dark bands, only with spotting or marbling (Fig. 14). Antennae reddish-brown (Kerney and Cameron, 1979). Body and sole mucus colorless and sticky. Keel usually well-marked. Internally the penis is large and convoluted (Barker, 1999).

Similar Species: In Kentucky, this species could be confused with the smaller, *L. valentiana* but the latter also has watery mucus and usually has distinct mantle bands (see above for extra detail).

D. Family Milacidae

Milax gagates (Draparnaud, 1801) – Figure 16

Global distribution: *Milax gagates* is thought to be native to the coasts and islands of the western Mediterranean and Canary Islands (Barker, 1999) but has been introduced to many parts of Europe including Ireland (Anderson, 2005), Great Britain (South, 1992) and Finland (Valovirta, 1969). It is an introduced species in North America (Fox, 1962; Chichester & Getz, 1973; Roth, 1986), Australia (Altena & Smith, 1975), New Zealand (Barker, 1999), Japan, South America and numerous Atlantic and Pacific Islands (Barker, 1999).

Ecology: This species is common in areas associated with people, such as gardens, agricultural fields (Kerney, 1966) and greenhouses (Valovirta, 1969). It is predominantly a subterranean species and is a pest of root crops (Barker, 1999). *Milax gagates* is also pestiferous in greenhouses (Gordon, 1994).

Description: Up to 5 cm in length (Barker, 1999). Body color usually gray to black (Fig. 16). Lateral bands absent. The keel runs from the end of the mantle to the tip of the tail and is usually of similar color to the body but in California Mc Donnell *et al.* (2009) collected specimens with a distinctly lighter colored keel. Body and sole mucus are colorless. Internally, the genital atrium contains a long and curved stimulator (Barker, 1999; Kerney and Cameron, 1979).

Similar Species: Although this is the only milacid collected in Kentucky, there are many similar species which are known pests in Europe. These include *T. budapestensis* which has recently been collected in the U.S. (Reise *et al.*, 2006). A dark median stripe on the sole (Pfleger, 1999) can be used to distinguish this species from *M. gagates. Tandonia budapestensis* also assumes a C-shape (Cameron *et al.*, 1983) when at rest or when threatened and it has no stimulator in the genital atrium (Barker, 1999). *Boettgerilla pallens* (Simroth) is also an invasive milacid (Kerney and Cameron, 1979). The slug is worm-like, bluish in color with a darker keel (Forsyth, 2004) and hence is very unlikely to be confused with any other species.

E. Family Testacellidae

(1) *Testacella haliotidea* Draparnaud, 1801 – Figures 3 and 17.

Remarks: Not yet recorded in Kentucky

Global distribution: *Testacella haliotidea* is native to Europe and North Africa (Barker, 1999) but outside of this region it has been introduced to North America and Cuba where it can be found in greenhouses (Chichester & Getz, 1973). It exists outside of greenhouses in Pennsylvania (Branson, 1976) and New Zealand (Barker, 1979). Roth and Sadeghian (2006) report the species from California and Barker (1999) from Australia.

Ecology: A carnivorous species feeding on invertebrates including earthworms, snails and other slugs (Barker, 1999). It spends most of its life underground, coming to the surface to hunt at night. *T. haliotidea* is most common in gardens and compost heaps (Cameron *et al*., 1986; Gordon, 1994).

Description: Up to 12 cm long with a small external shell located dorsally at the posterior end of the body (Fig. 3). Body color is yellow to grayish brown (Fig. 17) with colorless mucus. Two branched, lateral grooves originating from the anterior edge of the shell are a unique feature of testacellid slugs (Fig. 3). In *T. haliotidea* these grooves are separated by approximately 2 mm at their point of origin (Barker, 1999). Internally, the spermathecal duct is short and thick and the penis has an obvious flagellum (Quick, 1960).

Similar Species: The species with its external shell is unlikely to be confused with any other slugs in Kentucky.

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Acknowledgements

This research was funded by the Kentucky Science and Engineering Foundation as per Contract Agreement #KSEF-148-502-08-225 with the Kentucky Science and Technology Corporation. Rory Mc Donnell is supported by the European Union under a Marie Curie Outgoing International Fellowship (MOIF-CT-2005-21592) and James Harwood by the University of Kentucky Agricultural Experiment Station State Project KY008043. We are grateful to Lee Townsend, Doug Johnson, Ric Bessin and John Obrycki for comments on an earlier draft of the publication. Photographic credits: Roy Anderson (Queen's University of Belfast) (Figures 3, 6, 10, 12, 13, 16 and 17), Michal Maňas (Figure 14), Rory Mc Donnell (University of California – Riverside) (Figures 4, 5, 7, 8, 9, 11 and 15), James Harwood (University of Kentucky) (Figures 7, 9, 11) and Anna Thomas (University of Kentucky) (Figure 2).

Glossary of Terms

Echinate. Bearing or covered with spines or bristles; prickly.

Epiphallus. A sclerite in the floor of the genital chamber.

Flagellum. Finger-like projection on penis of certain slugs.

Foot fringe. Skin around foot of a slug.

Gastropod. Any mollusk of the class Gastropoda, comprising the snails, whelks, slugs, etc.

Genital pore. Opening from which the penis exits the body of a gastropod.

Hermaphrodite. Housing male and female sexual organs.

Keel. Raised tissue on the dorsal surface of some slugs.

Ligula. Strap-like structure used for stimulation in some gastropods.

Lineolations. Very fine parallel lines.

Mantle. A fold or pair of folds of the body wall that lines the shell and secretes the substance that forms the shell in mollusks and brachiopods.

Mollusca. Phylum containing gastropods, bivalves, cephalopods, and chitons.

Ocular tentacles. Tentacles on a mollusk which contain the visual organs.

Peduncular tentacles. Tentacles on a slug used for sensory perception.

Pneumostome. A small opening in the mantle of a gastropod through which air passes.

Figure 1. External slug morphology - A: head; B: ocular tentacle; C: penduncular tentacle; D: genital pore; E: foot fringe; F: tail; G: keel; H: pneumostome and I: mantle.

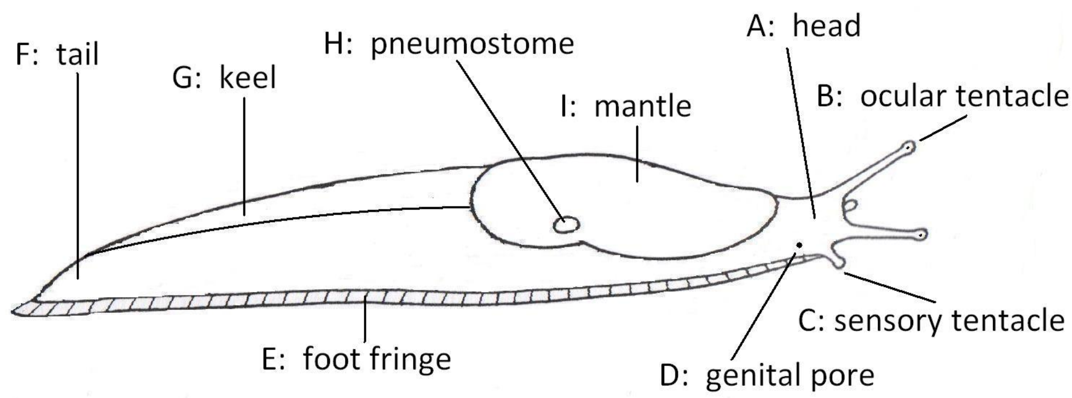

Figure 2. Genitalia of *Limax maximus* Linnaeus – A: penis (epiphallus in Arionidae); B: conjoint or hermaphrodite duct; C: spermathecal duct.

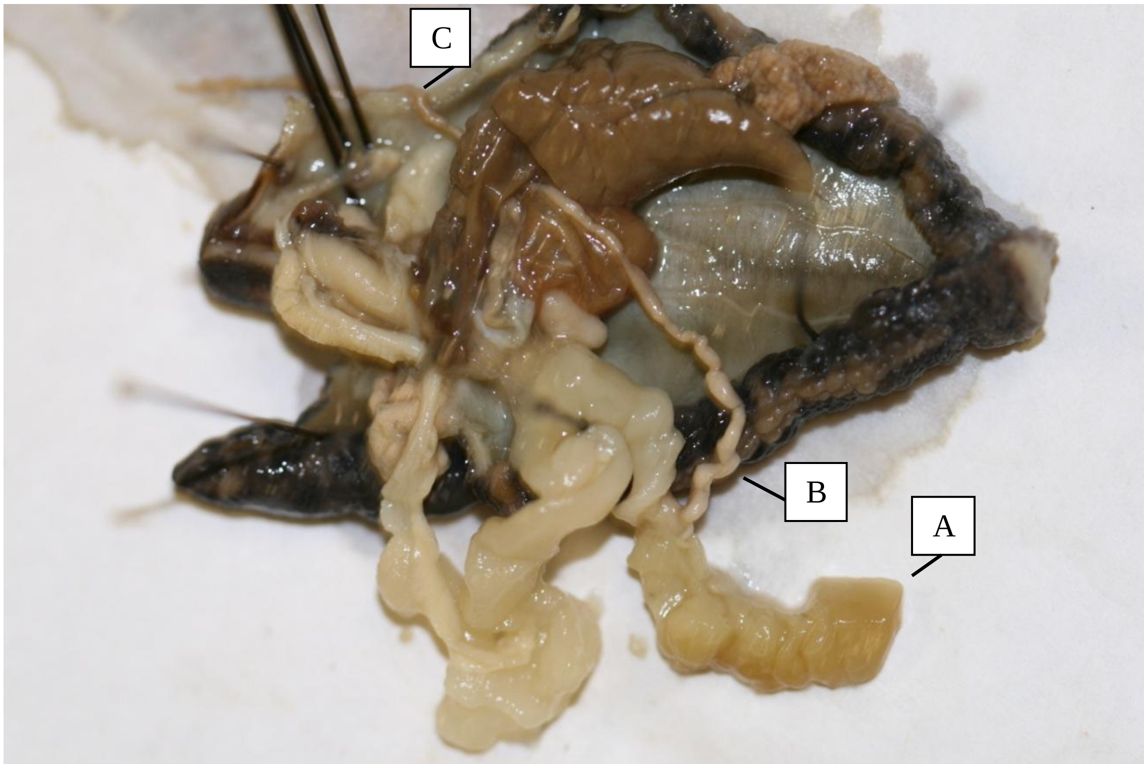

Figure 3. The externally located shell of *Testacella haliotidea* Draparnaud

Figure 4. *Arion subfuscus* (Draparnaud). Maximum length: 7 cm.

Figure 5. *Deroceras reticulatum* (Müller). Maximum length: 5 cm.

Figure 6. *Deroceras panormitanum* (Lessona and Pollonera). Maximum length: 3 cm.

Figure 7. *Deroceras laeve* (Müller). Maximum length: 5 cm.

Figure 8. *Arion rufus* (Linnaeus). Maximum length: 18 cm.

Figure 9. *Arion intermedius* Normand. Maximum length: 2.5 cm.

Figure 10. *Arion distinctus* Mabille. Maximum length: 4 cm.

Figure 11. *Arion hortensis* d'Audebard de Férussac. Maximum length: 5 cm.

Figure 12. *Arion fasciatus* (Nilsson, 1823). Maximum length: 5 cm.

Figure 13. *Limacus flavus* (Linnaeus). Maximum length: 5 cm.

Figure 14. *Limax maximus* Linnaeus. Maximum length: 20 cm.

Figure 15. *Lehmannia valentiana* (d'Audebard de Férussac). Maximum length: 7.5 cm.

Figure 16. *Milax gagates* (Draparnaud). Maximum length: 5 cm.

Figure 17. *Testacella haliotidea* Draparnaud. Maximum length: 12 cm.

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VITA of Anna K. Thomas

Date and Place of Birth:

- March 3, 1983, Baton Rouge, Louisiana, United States of America

Education:

- B.S. Biological Sciences (Minor: English), Louisiana State University, 2005

Professional Employment:

- Research Assistant, Department of Entomology, University of Kentucky, 2007-2009
- Laboratory Technician, Aquatic Invertebrates Laboratory, Auburn University, 2006
- Wildlife Biology Intern, United States Army Corps of Engineers, 2005

Publications:

- Mc Donnell, R.J., Thomas, A.K., and Harwood, J.D. (in preparation.). *A Field Guide to the Slugs of Kentucky*.

Presentations:

- Thomas, A.K. 2008. Faunistic survey of native and invasive slugs in Kentucky using morphological and molecular techniques. *Kentucky Society of Natural History spring conference*, Pine Mountain, KY.
- Thomas, A.K. and Harwood, J.D. 2008. Effects of dietary diversification on growth and development of the exotic terrestrial mollusk *Deroceras reticulatum*. *Annual meeting of the Entomological Society of America*, Reno, NV.

VITA of Anna K. Thomas cont'd.

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- Thomas, A.K., McDonnell, R.J., Obrycki, J.J., and Harwood, J.D. 2007. Comprehensive faunistic evaluation of native and invasive slugs in Kentucky. *Annual meeting of the Entomological Society of America*, San Diego, CA.

Scholastic and Professional Honors:

- Thomas, A.K. (P.I.): "Faunistic survey of native and invasive slugs in Kentucky using morphological and molecular techniques"; Kentucky Society of Natural History Student Research Grant, 2008-2009. ($450)
- Americorps Education Award, 2005
- TOPS (Taylor Opportunity Program for Students) Scholarship, 2001-2005